# Reproductive Seasonality of *Hypnea charoides* (Rhodophyta) and Algal Recruitment in Ping Chau, N.T., Hong Kong SAR, China

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in

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*In the Memory of*

*My Grandfather*

*Dedicated to My Family*

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# Abstract

Seasonal growth and reproduction of a marine red alga, *Hypnea charoides,* and recruitment of marine algae were investigated along the shores of A Ma Wan (AMW) and Lung Lok Shui (LLS) in Ping Chau, N. T., Hong Kong SAR, China, from 1996 to 1999.

Populations of *H. charoides* in AMW and LLS generally occurred in winter and spring (November to April) but disappeared during summer and fall from 1996 to 1999. Mean length of *H. charoides* in AMW was significantly negatively correlated with photoperiod ($r = -0.359$) and seawater temperature ($r = -0.669$) but was not correlated with any nutrient concentration in seawater. Plants were mostly vegetative but relatively high abundance of tetrasporic plants was observed at the end of each growing season. Percentage occurrence of tetrasporic plants was significantly positively correlated with seawater temperature in samples collected from attached populations at –1 m CD ($r = 0.635$) and –2 to –3 m CD ($r = 0.690$) and from drifted populations ($r = 0.705$), suggesting that increase in seawater temperature might induce tetrasporogenesis of *H. charoides* in AMW. In LLS, most of the plants were vegetative but 100 % were tetrasporic in samples collected at –1 m CD during an unusual growth period in October 1998. High abundance of tetrasporic plants was also observed at a depth of –10 m CD on 9-Apr 1998 (97.5 %) and 22-Apr 1999 (90 %). Dominance of vegetative and tetrasporic plants and rarity of cystocarpic plants in both AMW and LLS suggested that the lifespan of *H. charoides* might be very short and/or majority of the plants underwent apomeiosis to complete their life cycles in Ping Chau.

Algal recruitment was studied by artificial clearings, artificial substrata and seasonal collection of seawater. Two types of clearing plots (chiselled vs hammered) were created and observed monthly on the rocky shores in AMW from November 1997 to June 1999. Similar recruitment patterns shown in chiselled, hammered and control plots indicated that marine algae in A Ma Wan were mostly recruited but not regenerated from remnants of preceding year. Pronounced annual variations were observed in the species composition and percentage cover of the algal recruits, implying that recruitment and growth patterns of marine algae in a specific place may vary significantly between years. However, all variations in patterns of recruitment would finally terminate at the same point of stability after summer die-off.

Setting up artificial substrata (ceramic tiles) from January 1998 to May 1999 allowed an examination of the early algal assemblages in Ping Chau. Algal recruits were observed throughout the whole study period. Significant temporal variations were found in the recruitment patterns shown on biweekly- and monthly- retrieved tiles with respect to algal species composition, species richness, mean density, percentage cover of encrusting coralline algae and species diversity. Similar recruitment patterns between these tiles and a few records of adult plants on the permanently-placed tiles indicate a high mortality of algal recruits during the recruitment process.

Seawater samples, seasonally collected at –1 m CD, –2 to –3 m CD and –10 m CD in both AMW and LLS (September 1998 to May 1999), showed that algal spores were available throughout the year. Significant seasonal differences in terms of percentage frequency and species diversity in AMW and LLS indicate that there are

temporal and spatial variations in the availability of algal spores. Relatively high frequencies of algal recruits were recorded at –1 m CD and –2 to –3 m CD in AMW in spring, coinciding with the period of high number of fertile marine algae.

In Ping Chau, the success of a new algal growth season may largely depend on the availability of the propagules in the water column or the perennation of old remnants persisting as turfs. In effect, both sexual and asexual reproductions play critical roles in the population dynamics of *H. charoides* in Ping Chau.

# 摘要

此碩士論文旨在研究香港的一種紅海藻—*Hypnea charoides*—的季節性生長和繁殖，以及其他海藻的新添量，實驗地點是位於香港東北面的平洲其中兩個岸灘—亞媽灣和龍落水。

平洲的 *H. charoides* 於每年的冬季和春季（約 11 月至 5 月）生長，在過去三年的研究期間（1996 至 1999 年），亞媽灣的 *H. charoides* 的平均長度跟光照期和海水溫度有明顯的負關係。研究結果顯示，這些個體大部份都是營養體，但每年的生長季節後期卻有相對較多的四分孢子體，而且在不同水深所採的樣本當中，四分孢子體的出現百分比均與海水溫度有明顯的直接關係（水深 1 米處的 r 值爲 0.635；2 至 3 米處爲 0.690；漂浮樣本爲 0.705）。這表示 *H. charoides* 可能在水溫較高的情況下製造較多的四分孢子。生長在龍落水的個體大部份也是營養體，但在 1998 年 10 月所採的樣本均屬四分孢子體，而在 10 米水深的個體亦有較多的四分孢子體（1998 年 4 月爲 97.5 %；1999 年 4 月爲 90 %）。研究期間並不常發現囊果，這可能是平洲的 *H. charoides* 的生命週期很短暫，這使其配子體相對地較難找到，另外亦有可能是其四分孢子以不完全減數分裂發育成爲一棵新的四分孢子體，而沒有經過配子體的階段。

此論文的另一部分是研究平洲海藻的新添量。首先在亞媽灣的天然石基上製造一對不同的小地，一是將石面的生物清除，另一塊則將石面擊碎。從 1997 年 11 月至 1999 年 6 月所進行的實驗結果顯示，兩種經不同處理的石基所新添的海藻情況均沒有顯著的差異，但 1998 年海藻的新添量卻明顯跟 1999 年的不同，這表示平洲的海藻是以不同形式新添在石基上（如配子、孢子等）而不是從上一季遺留在石面上的海藻重生的，並且在同一處地方，海藻的新添量情況並非每年都是一樣的。

除了利用天然地基，1998 年 1 月至 1999 年 5 月期間亦有在亞媽灣和龍落水的海底放置一些人工營養基（瓦片）。結果顯示所有瓦片均新添了一些細微的海藻，這些在每兩星期取出和每一個月取出的瓦片上新添的海藻，其物種成分、數目、密度、珊瑚狀海藻的覆蓋百分比和多樣性均有時間上的差異，但這兩種瓦片之間卻沒有顯著的分別，另外，在海底觀察的瓦片中並沒有發現很多海藻生長，這表示了新添的海藻的死亡率可能很高。

此外，在 1998 年 9 月至 1999 年 5 月期間所取的海水樣本（取水地點分別是亞媽灣和龍落水的水深 1 米、2 至 3 米以及 10 米處）顯示，平洲的水域整年間都有海藻的孢子或繁殖芽，此外，新添海藻的出現百分比和多樣性均在時間上和地區上有顯著的差異，而春天時在亞媽灣水深 1 米和 2 至 3 米處所採的樣本中更記錄了較多的海藻，這正配合了每年平洲海藻生長的盛季。

總括來說，每年平洲海藻的生長主要是依賴海水中的孢子或繁殖芽，亦有可能是重生自遺留在石面上的海藻，至於 *H. charoides*，除了有性繁殖外，無性繁殖亦對其種群的延續扮演著重要的角色。

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# Chapter 1

# General Introduction

## 1.1 Introduction

Algae are a group of photosynthesizing organisms ("lower plants") lacking true leaves, stems and roots. They are found almost everywhere, including marine, freshwater, brackish and terrestrial environments, or some are even air borne. Their sizes range from microscopic to macroscopic. The smallest known alga, *Micromonas pusilla*, is only 1 x 1.5 μm in size while certain species of kelp may attain a length of 65 m (Bold *et al.* 1987). For those algae which are marine and with macroscopic plant body, they are sometimes regarded as "seaweeds". Based on their differences in pigmentation, nature of stored food reserves, cellular structure, chemical composition and reproduction patterns, algae can be divided into many divisions, traditionally with Chlorophyta (green algae), Phaeophyta (brown algae) and Rhodophyta (red algae) being the three main groups. In recent years, algal taxonomists also examined the molecular sequence or genome architectural information of algae. Based on these additional criteria, recent classification scheme divides algal species into nine divisions. They are: Cyanobacteria, Glaucophyta, Euglenophyta, Crytophyta, Haptophyta, Dinophyta, Ochrophyta (including brown algae), Rhodophyta and Chlorophyta (see Graham & Wilcox 2000).

Majority of the marine algae are rhodophytes. Over 10,000 of them have been described, but how many species there really are in the world still remains unanswered (Woelkerling 1990). Though red algae occur in such a great number, their biological significance is only beginning to be appreciated in recent decades.

More than 20 years ago, Dixon (1973) reviewed the many different aspects of red algae, e.g. their structure, morphology, reproduction and life histories, economic utilization and systematics, and finally concluded that Rhodophyta was probably the worst known of any algal group. More recently, Murray & Dixon (1992) re-evaluated some of these aspects and found more than 7000 original research articles that appeared in the literature during the past two decades. Undoubtedly, there is a tremendous increase in the number of investigators interested in understanding the biology of red algae.

Algal ecology is one of the most neglected aspects of the biology of red algae, more particularly reproductive ecology, recruitment and survivorship of red algal populations (Kain & Norton 1990). One of the underlying problems is the difficulty to observe and understand the obscure and ephemeral events in their sexual cycle (e.g. the time of formation, location, and nature of the generative auxiliary cell) (Woelkerling 1990). Red algae exhibit relatively complicated method of reproduction when compared to other algal groups. They are completely devoid of flagellate cells in any stages of their life cycles. Most members have a triphasic life cycle. The three growth phases include one gamete-producing sexual phase (gametophyte generation) and two spore-producing asexual phases (tetrasporophyte and carposporophyte generations). In many species, records on male and/or female plants have never been made, and for some, information on sexual reproduction is virtually not available (Woelkerling 1990). Hence, considerable information is needed in order to have a better understanding of red algal reproductive ecology.

Many red algae (at least 344 recognized species, Tseng 1981) are of much economic importance. They have been consumed by humans for more than 2,800 years (see

Waaland 1981). They are also used for the production of colloid-forming polysaccharides found in the cell walls, such as agar, agarose and carrageenan. Many phycocolloid producers come from members of the order Gigartinales. Due to this reason, some members, such as *Hypnea* spp., are in much commercial demand.

Many species of *Hypnea* are used as human food, animal feed and as one of the sources of antibiotic and antitumor agents (Trono 1997). Several species, more particularly *H. musciformis*, are used as raw materials in the production of agar and/or carrageenan (Humm & Williams 1948, Chapman 1970, Mshigeni 1977, Rama Rao 1977, Waaland 1981, Guist *et al.* 1982, Friedlander & Zelikovitch 1984, Schenkman 1989, Reis & Yoneshigue-Valentin 2000). The importance of *Hypnea* spp. is thus quite well known. However, although *Hypnea* is a ubiquitous genus of tropical seas, complete life histories are not known for many members in the family Hypneaceae (West & Hommersand 1981). Besides, *Hypnea* is regarded as one of the most taxonomically difficult genera in Rhodophyta as it exhibits wide variability in gross morphology among many closely related entities (Chiang 1997, Xia & Wang 1997, Yamagishi & Masuda 1997, see also Kraft 1981 & Abbott 1997), indicating a need to study its biology.

In Hong Kong, *Hypnea* is one of the most abundant marine algae. Other species, like brown algae *Padina* spp. and *Sargassum* spp., green algae *Enteromorpha* spp. and *Ulva* spp., and red algae *Corallina* spp., are also common along many coastal shores. The diversity, abundance and zonation patterns of many intertidal algae are affected by the monsoonal nature of Hong Kong's climate (Kennish *et al.* 1996, Kaehler & Williams 1996). Strong afternoon illumination coinciding with extreme

low tides during summer significantly reduce the survival rates of most algae such that they disappear in summer and grow only in late fall to spring (Hodgkiss & Lee 1983, Hodgkiss 1984). Environmental factors are also important in affecting the early development of algal assemblages (Kaehler & Williams 1998) as well as the abundance of encrusting algae (Kaehler & Williams 1997). While these few studies provided some insights on the ecology of intertidal algae in Hong Kong, little is known about their reproduction and life histories, specifically, how they respond to different environmental conditions. Information on the abundance and dominance of certain subtidal algal species, such as *Hypnea* spp., in many coastal waters in Hong Kong are even more limited. Therefore, knowledge about the seasonal occurrence, reproduction, recruitment and growth patterns of these shallow subtidal populations of marine algae and the possible existence of algal propagules in water column are matters worth pursuing, in order to understand the dynamics of these shallow water algal communities.

## 1.2 Study Site

Ping Chau is an outlying island located in the northeastern part (114°26'E and 22°33'N) of the New Territories, Hong Kong SAR, China (Fig. 1.1). Due to its relative remoteness, Ping Chau is subjected to relatively few human disturbances and pollution. It is famous for its rock formation. The rocky substratum, mostly made of siltstone, supports growth of many different kinds of marine organisms such as corals, molluscs, reef fishes and marine algae. Due to its relatively high biodiversity and the abundance of these marine organisms, Ping Chau was designated as a marine park on 16$^{th}$ November 2001 in order to conserve its valuable environments. However, until recently, there are only a few records of studies done on the marine environment in Ping Chau (Morton & Morton 1983, Morton 1988,

Scott 1984).

A Ma Wan and Lung Lok Shui, which face the northeast and southwest respectively, are two coastal shores along the island. A Ma Wan is a sheltered beach that is surrounded by extensive coral communities. In contrast, Lung Lok Shui is very exposed and is subjected to strong waves generated by the SE monsoon during summer months. An extensive bed of seaweeds is found in Lung Lok Shui in cooler months, dominated by *Sargassum* spp.

## 1.3 Study Material

Populations of *Hypnea charoides* were chosen for the present study because of their abundance in Ping Chau, particularly in A Ma Wan and Lung Lok Shui during winter months. Their biology has never been studied in Hong Kong.

The generic name "*Hypnea*" refers to the mosslike appearance of the plants. Its life history is of the *Polysiphonia*-type in which isomorphic, dioecious gametophytes and tetrasporophytes occur and a diploid carposporophyte develops on the female gametophyte (Masuda *et al.* 1997, see also Murray & Dixon 1992). Both the cystocarps and tetrasporangia, if present, are swollen and densely arranged on the branches. Tetrasporangia in all members of the family Hypneaceae are zonate (Guiry 1990).

Two species of *Hypnea*, *H. charoides* and *H. japonica*, have been reported from Hong Kong (Hodgkiss & Lee 1983), with the former being more common. It is a common economic marine alga used for food. The thallus is brownish to pale red but sometimes appears to be pale or dark green. Plants are usually more than 20 cm

tall and become entangled in a mass. Unlike *H. japonica*, *H. charoides* does not produce hamate (hooked) branches that function as tendrils, allowing this alga to cling onto other algae. Populations of *H. charoides* in Ping Chau are found either loosely attached on the rocky substratum in clumps or entangled with other algae (e.g. *Sargassum* spp.) (Fig. 1.2). Many individuals, however, are easily swept away by current and thus become drifted in the water column.

## 1.4 General Objectives

The general objectives of this thesis are:

1. To study the seasonal occurrence and reproduction of *Hypnea charoides* in relation to variation in certain environmental parameters (e.g. photoperiod, seawater temperature and nutrient concentrations in seawater).

2. To understand the recruitment and growth patterns of *H. charoides* as well as those of other algae in Ping Chau.

## 1.5 Organization of the Thesis

The organization of this thesis is as follows:

**Chapter 1** reviews some background information on what algae are (focusing on red algae), the economic importance of algae, the genus *Hypnea*, phycological studies in Hong Kong, the study site "Ping Chau", the general objectives as well as the organization of this thesis.

**Chapter 2** studies the seasonal occurrence and reproduction of *Hypnea charoides* in A Ma Wan and Lung Lok Shui in Ping Chau in relation to changes in several environmental parameters such as photoperiod, seawater temperature and nutrient concentrations in seawater.

**Chapter 3** investigates the growth and recruitment patterns of marine algae in A Ma Wan by artificial clearings, focusing mainly on the species composition and percentage cover between two growing seasons.

**Chapter 4** deals with the seasonal patterns of the colonization of early algal assemblages on artificial substratum (ceramic tiles) in A Ma Wan.

**Chapter 5** examines the availability of algal propagules in water column at different depths in both A Ma Wan and Lung Lok Shui by seasonal collection of water samples.

**Chapter 6** concludes the findings from different experiments of the present research and tries to explain the reproductive seasonality of *H. charoides* as well as the recruitment patterns of marine algae in Ping Chau.

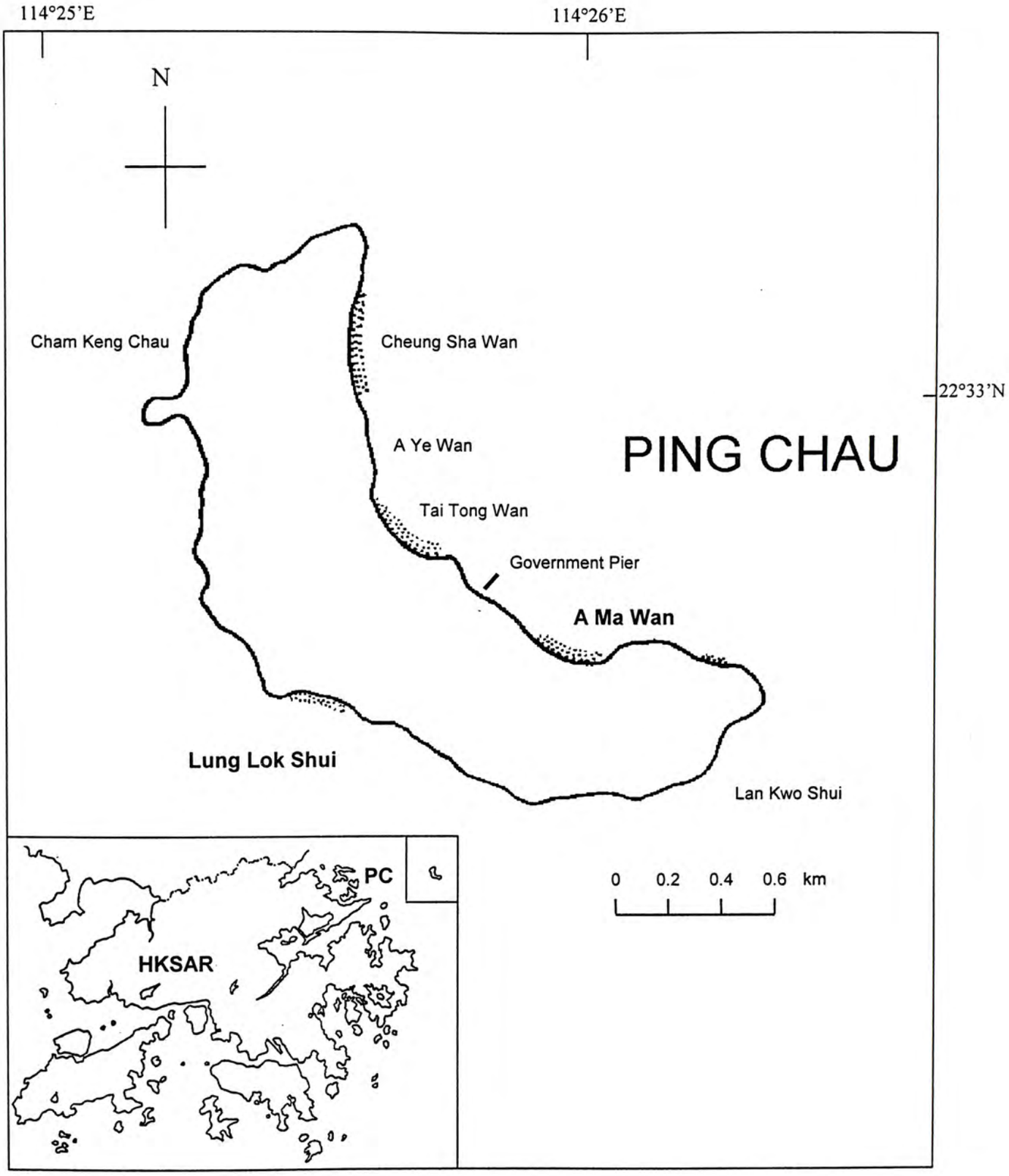


Fig. 1.1. Map of Ping Chau, showing the locations of A Ma Wan and Lung Lok Shui. The location of Ping Chau (PC) is shown in the insert map of Hong Kong SAR (HKSAR).

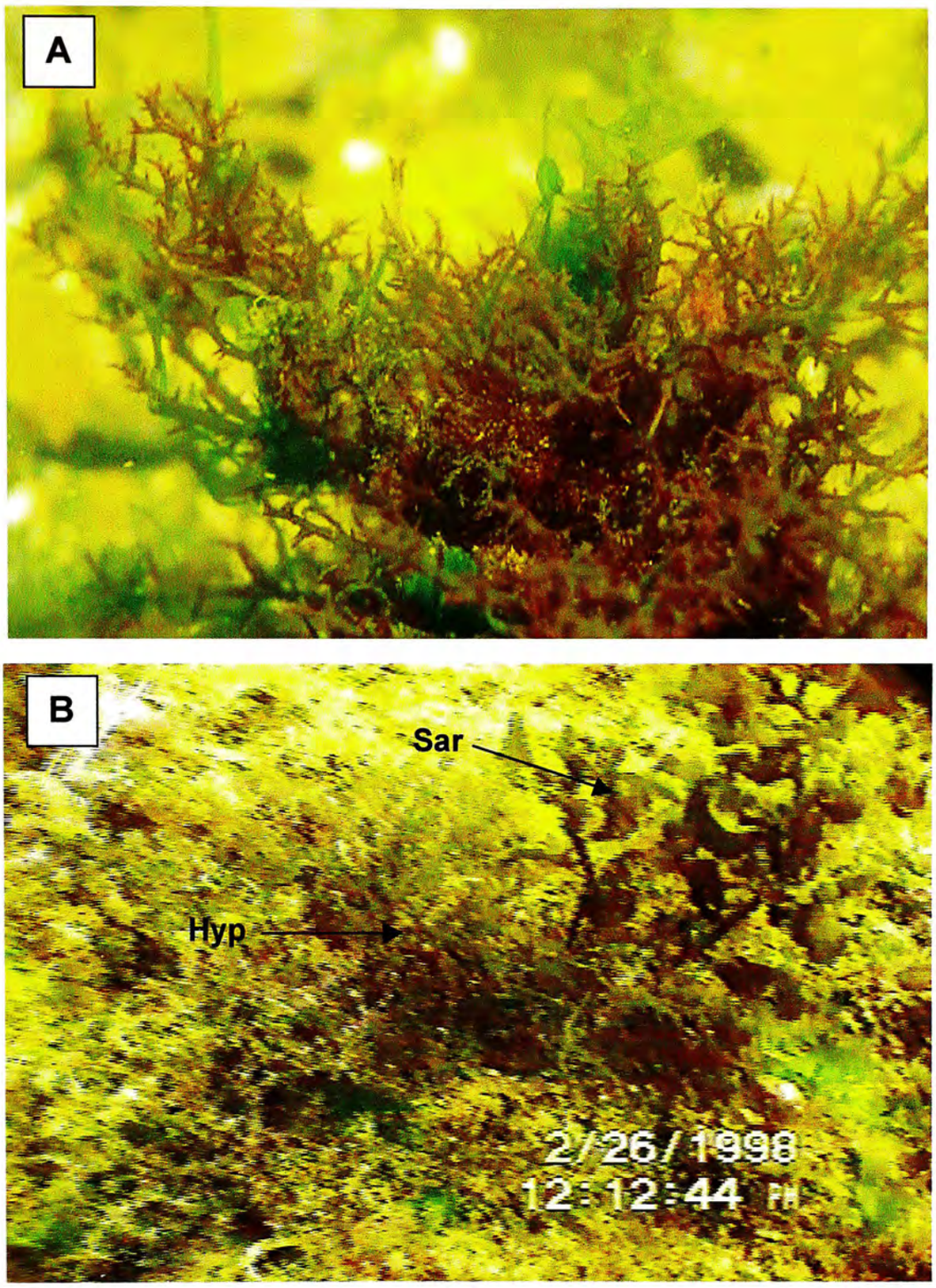


Fig. 1.2. Living habits of *Hypnea charoides* and other algae in A Ma Wan. (A) Living habits of *H. charoides*; (B) clumps of *H. charoides* (Hyp) found entangled with the holdfast of *Sargassum* spp. (Sar)

# Chapter 2

# Seasonal Occurrence and Reproduction of *Hypnea charoides* in Ping Chau

## 2.1 Introduction

The study of plant community ecology has two main purposes, the analysis of patterns and the elucidation of the forces that determine these patterns. In a marine ecosystem, algae (microscopic and macroscopic) and seagrasses play very important roles in structuring the whole community as they are the dominant primary producers in the system. Hence, their population dynamics greatly affect those of all the other organisms. However, little attention has been paid in this aspect in algal vegetation studies. For population dynamic analysis, seasonal growth and reproduction have been of considerable interest to many phycologists. They are known to be closely tied to changes in different environmental conditions and the availability of resources. Among these parameters, light and temperature are the physical factors which have been most widely investigated with respect to the growth and reproductive responses of marine algae (Burns & Mathieson 1972a, b, Adey 1973, Mathieson & Burns 1975, De Wreede 1976, Kapraun 1978, Prince & O'Neal 1979, Schoschina *et al.* 1996, Voskoboinikov *et al.* 1996, Zamorano & Westermeier 1996, Vásquez *et al.* 1998). This is particularly so in many red algal species where irradiance and photoperiod have received the greatest attention as factors that control their reproductive processes. Out of the 46 red algae examined by various authors, 38 species showed that the development or release of their reproductive structures was a type of photoperiodic responses (see review by Murray & Dixon 1992). Many of these responses were also associated with changes in temperature and some, in nutrient levels. This indicates that temperature or nutrient concentrations could modify or block the inductive effects

of photoperiod. Ranges of temperature, irradiance, or photoperiod can therefore serve as thresholds that trigger growth or reproduction in many algae.

Many marine red algae have triphasic life cycle characterized by a diploid generation of tetrasporophyte, a haploid generation of gametophyte and a diploid generation of carposporophyte that develops on the female gametophyte. Natural populations of these algae do not always have equal proportions of these generations at any one time. The dominance of one generation (phase) over the other is commonly reported. For example, gametophyte was reported to be the dominant generation in populations of *Iridaea cordata* (May 1986), *Chondrus crispus* (Laura Lazo *et al.* 1989) and *Gigartina skottsbergii* (Piriz 1996, Zamorano & Westermeier 1996), whereas tetrasporophyte was dominant in other populations of *Iridaea cordata* (Hansen & Doyle 1976), *Gracilaria bursapastoris* and *G. coronopifolia* (Hoyle 1978), *Callithamnion corymbosum* (Whittick 1978), *Gelidiopsis variabilis* (Kaliaperumal & Umamaheswara Rao 1982), *Hypnea musciformis* (Schenkman 1989), *Bostrychia tenella, Caloglossa leprieurii* and *Catenella impudica* (Narasimha Rao 1995), and *Rhodymenia howeana* (Vásquez *et al.* 1998). Several hypotheses have been advanced to explain the significance of these differences in phase dominance as part of the life history strategy of these algae. Environmental factors, such as temperature, photoperiod, irradiance, have also been shown to affect phase dominance in different seasons within a year (Dyck & De Wreede 1995, Piriz 1996, see also review by Murray & Dixon 1992).

Hong Kong is located in the southeastern part of China. It experiences a subtropical, highly seasonal monsoonal climate with annual die-off of the intertidal epibiota (Williams 1993). The weather in summer (June to August) is hot (mean air

temperature = 30 °C) and wet while that in winter (December to February) is cool (mean air temperature = 17 °C) and dry (Kennish *et al.* 1996, see also Hodgkiss 1984). This characteristic monsoonal climate also brings about marked differences in the seawater conditions (more particularly in temperature). Being an important component of many coastal communities, most intertidal marine algae in Hong Kong display clear seasonal patterns in which they start to grow in winter and disappear in summer (Hodgkiss & Lee 1983). Their diversity, abundance or zonation patterns were strongly influenced by the monsoonal nature of Hong Kong's climate (Kennish *et al.* 1996, Kaehler & Williams 1996) and strong sunlight was suggested to be the major factor responsible for their seasonal pattern of distribution (Hodgkiss 1984). Nonetheless, distribution patterns of subtidal algal populations have never been studied in Hong Kong except for some anecdotal observations. In Ping Chau, on the northeastern part of Hong Kong, for example, subtidal populations dominated by *Hypnea charoides* also show a seasonal pattern in both their occurrence and reproduction. Details of this seasonal pattern, especially with respect to the occurrence and abundance of different reproductive stages (phases) are, however, not known.

This study investigated the seasonal growth and reproduction of *H. charoides* in Ping Chau with an attempt to relate these seasonal patterns with the variations in photoperiod and seawater conditions, e.g. temperature and nutrient concentrations. This is the first study of its kind in Hong Kong waters.

## 2.2 Materials and Methods

### 2.2.1 Study sites

Field experiments were carried out in both A Ma Wan and Lung Lok Shui, Ping Chau.

A Ma Wan, which is facing the northeast, is a more sheltered area, while Lung Lok Shui, located on the southwest side of the island, is very exposed and subjected to strong waves generated by the SE monsoon. In winter, a number of algal species grow densely on the siltstone substratum, which forms a series of slightly inclined terraces (15° to 20°) lying perpendicularly to the shore, at a depth of –1 to –3 m CD in A Ma Wan. These marine algae include *Colpomenia sinuosa*, *Dictyota* spp., *Enteromorpha* spp., *Galaxaura fruticulosa*, *Hypnea* spp., *Padina arborescens*, *P. australis*, *Sargassum* spp. and *Ulva* spp., with *Hypnea charoides* being one of the most dominant red algal species observed. Areas beyond –3 m CD are dominated by coral communities. In Lung Lok Shui, the siltstone substratum also forms inclined terraces (15° to 20°) but in contrast to A Ma Wan, *Sargassum* spp. are the most dominant, canopy-forming species grown on these terraces. Compared with A Ma Wan, marine algae in Lung Lok Shui are far more dominant than corals, with populations growing from –1 to –10 m CD.

### 2.2.2 Populations of *Hypnea charoides*

Individuals of *Hypnea charoides* are either loosely attached on the rocky substratum forming clumps or are entangled with other marine algae (e.g. *Sargassum* spp.). Many of them, however, are easily swept away by waves and thus become drifted in the water column. Comparatively, more attached and drifted individuals were observed in A Ma Wan. An attached population of *H. charoides* is found on the inclined terraces at –1 m CD while another grows on the corals (alive or dead) at –2 to –3 m CD. Drifted individuals mostly occur at a depth of –2 to –3 m CD. In Lung Lok Shui, most of the clumps were found entangled with the holdfast of *Sargassum* spp. on the terraces at –1 to –3 m CD while a much deeper population was observed at a depth of –10 m CD.

### 2.2.3 Measurement of plant length

Measurement of plant length and sample collection of *Hypnea charoides* were carried out by SCUBA or by snorkeling in both A Ma Wan and Lung Lok Shui. One hundred individuals (clumps) were haphazardly selected and measured at a depth of –1 to –2 m CD every two weeks from January 1997 to June 1999 in each site. Plant length was measured from the base to the tip of each clump of *H. charoides*. Due to typhoons or strong monsoon, field trips were sometimes interrupted (especially to Lung Lok Shui). Therefore, *in situ* length measurement could not be carried out regularly at exactly biweekly intervals and at times, had to be delayed for one or two weeks. All the plants measured in A Ma Wan were attached individuals while those in Lung Lok Shui were individuals entangled with the holdfasts of *Sargassum* spp.

### 2.2.4 Examination of reproductive structures

To examine the reproductive structures of *Hypnea charoides*, samples were collected at approximately biweekly intervals during the growing seasons from January 1996 to June 1999. At each sampling in A Ma Wan, 30 attached individuals (clumps) were haphazardly collected from the population on the siltstone substratum at a depth of –1 m CD and another 30 were from the population on corals at depths of –2 to –3 m CD. Additional drifted samples (30 individuals at each sampling) within the water column of –2 to –3 m CD were also collected. Starting in 1999, an extra 30 attached samples were collected approximately biweekly (February to April) at a depth of –5 m CD for further examination. In Lung Lok Shui, 30 drifted individuals entangled with *Sargassum* spp. (fronds or holdfasts) were collected at depths of –1 to –2 m CD. Starting from April 1998, additional samples (30 individuals at each sampling) were collected from a depth of –10 m CD. All the plants collected were taken back to the laboratory and examined under the microscope for the presence or absence of

reproductive structures (cystocarps vs tetrasporangia). The occurrence of different reproductive stages (phases) was expressed as a percentage of the number of cystocarpic, tetrasporic or vegetative plants over the total number of plants observed.

### 2.2.5 Environmental parameters

Information on photoperiod over the sampling period was obtained based on the sunrise and sunset data from the Hong Kong Observatory. Seawater temperature was recorded by temperature probes (Minilog TP, Vemco Inc., Halifax, Canada) in both A Ma Wan and Lung Lok Shui over the study period. These probes were set to record the bottom temperature every 30 minutes and were retrieved for replacement approximately every other month. In A Ma Wan, the temperature probe was placed at a depth (–1 to –2 m CD) in between the –1 m CD and –2 to –3 m CD populations. There was no significant difference in the seawater temperature between –1 m and –3 m CD. Hence, only one set of temperature data was collected. In Lung Lok Shui, three temperature probes were placed respectively at depths of –1 m CD, –2 to –3 m CD and –10 m CD. However, due to strong waves and possible human interferences, temperature probes at –1 m CD were frequently lost. So, only data recorded at –2 to –3 m CD and –10 m CD were available. For nutrient analysis, three water samples (mostly surface water) were collected from A Ma Wan and Lung Lok Shui at approximately biweekly intervals. Concentrations of ammonium ions, nitrites, nitrates and phosphates were determined by an autoanalyzer in the laboratory using the standard methods prescribed the American Public Health Association (APHA 1995).

### 2.2.6 Statistical analysis

Pearson Product Moment Correlation (SigmaStat, Jandel Scientific Software) was used to correlate the patterns of changes in mean plant length and percentage

occurrence of reproductive phases with variations in the environmental parameters investigated.

## 2.3 Results

### 2.3.1 Seasonal occurrence and growth of *Hypnea charoides*

#### 2.3.1.1 A Ma Wan populations

Populations of *Hypnea charoides* in A Ma Wan were observed from January to May in 1997, from January to April in 1998 and from December 1998 to May in 1999 (Fig. 2.1). Mean plant length (± SD) was first measured in January 1997. It reached its maxima on 16-Feb 1997 (17.0 ± 9.5 cm), 11-Apr 1998 (11.7 ± 6.8 cm) and 21-Mar 1999 (14.0 ± 4.0 cm) and minima on 8-Mar 1997 (10.6 ± 4.5 cm), 24-Jan 1998 (4.8 ± 2.0 cm) and 11-May 1999 (4.1 ± 1.3 cm) respectively in the three growing seasons from 1996 to 1999 (Fig. 2.1). The population usually appeared as creeping thalli or as very short branches at the start or the end of each growing season.

#### 2.3.1.2 Lung Lok Shui populations

In Lung Lok Shui, *Hypnea charoides* normally appeared within the same period as in A Ma Wan, from January to May in 1997, January to April in 1998 and from January to April in 1999 (Fig. 2.2). However, many individuals were also observed from July to December in 1998 during an unusual sudden bloom. Plant length measurement started in January 1997. The maximum values were 12.8 ± 6.1 cm on 3-May 1997, 10.0 ± 5.7 cm on 22-Apr 1998 and 20.1 ± 6.1 cm on 22-Apr 1999 while the minimum values were 10.9 ± 4.1 cm on 28-Mar 1997, 6.0 ± 2.2 cm on 16-Mar 1998 and 4.7 ± 1.9 cm on 23-Feb 1999 respectively in the three growing seasons from 1997 to 1999 (Fig. 2.2).

In July 1998, the population of *H. charoides* in Lung Lok Shui appeared as short branches entangled around the bases of *Sargassum* spp. This growth period was much earlier than what was normally observed. At the end of September, plants were observed to have two growth forms: prostrate and erect. The prostrate parts appeared like a vegetative mat adhering onto the rocky substratum whereas the erect parts were long and bushy. Both of them exhibited healthy greenish red in coloration. They grew so rapidly and covered almost the whole area that was normally dominated by *Sargassum* spp. at that period of time. Measurement was done on the erect plants only once on 11-Oct 1998 (12.2 ± 4.9 cm) as all these plants disappeared during the following visit to Lung Lok Shui in November 1998. Only short creeping branches were observed thereafter (November 1998 to January 1999).

### 2.3.2 Reproductive seasonality

#### 2.3.2.1 A Ma Wan populations

During the period from 1996 to 1999, the –1 m CD attached population of *Hypnea charoides* in A Ma Wan appeared in winter and early spring and disappeared completely in the summer (Fig. 2.3). All the plants observed from December 1996 to February 1997 were vegetative. Tetrasporic plants were first observed on 23-Mar 1997 and 15.9 % of the plants were tetrasporic. This percentage occurrence increased to 50 % on 13-Apr 1997. The next growing season (starting from January 1998) also showed dominance in vegetative plants and 13.3 % of the plants were tetrasporic on 11-Apr 1998. This percentage increased to 60 % on 25-Apr 1998. Cystocarpic plants were rarely seen and found only on 13-Dec 1998 (6.7 %). When compared with the previous two growing seasons, the percentage occurrence of tetrasporic plants was relatively low during the growth period in 1999, with a maximum of 30 % recorded on 3-Apr 1999.

Drifted and attached samples at –2 to –3 m CD were collected for examination starting from 1997 and 1998 respectively (Figs. 2.4 & 2.5). Drifted samples were first collected in March 1997 and majority of them were vegetative (Fig. 2.4). Percentage occurrence of tetrasporic plants increased from 3.3 % (23-Mar) to 56.7 % (13-Apr) in 1997 and cystocarpic plants were only recorded on 23-Mar (3.3 %). In 1998, no cystocarpic plants were observed and tetrasporic plants were only found in April, with an increase from 60 % (11-Apr) to 82.8 % (25-Apr). However, cystocarpic plants occurred quite frequently in the growing season from December 1998 to March 1999. In spite of this, the percentage occurrence of cystocarpic plants remained very low, ranging from 3.3 % on 21-Feb 1999 to 8.3 % on 13-Dec 1998. Similarly, tetrasporic plants were found in all the samples collected in the second growing season, ranging from 3.3 % on 21-Feb 1999 to 58.3 % on 13-Dec 1998.

For attached samples at –2 to –3 m CD, majority of the plants were vegetative (Fig. 2.5). A few cystocarpic plants were observed on 3-Feb (3.3 %) and 25-Apr (6.5 %) in 1998. Tetrasporic plants were only found in April 1998 with a maximum percentage of 90 % on 25-Apr. In the second growing season from December 1998 to April 1999, however, they were present in all the samples collected, ranging from 3.3 % on both 7-Feb and 7-Mar 1999 to 50 % on 3-Apr 1999.

All the plants (100 %) collected at a depth of –5 m CD in 1999 from A Ma Wan were vegetative in February (Fig. 2.6). This percentage occurrence dropped to 6.7 % on 3-April when majority (83.3 %) of the plants became tetrasporic. Only few cystocarpic plants (10 %) were observed on 3-Apr 1999.

2.3.2.2 Lung Lok Shui populations

In Lung Lok Shui, the population of *Hypnea charoides* at –1 to –2 m CD appeared in January and disappeared in May 1997 (Fig. 2.7). Majority of the plants were vegetative and 23.3 % of them were tetrasporic on 29-Mar 1997. This percentage increased to 46.7 % on 3-May 1997. In 1998, all the plants (100 %) observed in February and March were vegetative but 80 % of them were tetrasporic on 22-Apr 1998. In July 1998, when some individuals reappeared apparently earlier than normal as small clumps, all of them (100 %) were vegetative. In September, however, they grew very quickly and 41.7 % of the plants were tetrasporic. By October, all of them (100 %) were tetrasporic. After this period, there were only creeping parts left behind. Tetrasporic plants were observed again in the following January 1999 (23.3 % on 3-Jan) and this percentage occurrence rose to 66.7 % on 22-Apr 1999. No cystocarpic plants were found in Lung Lok Shui during the whole study period.

Samples of *H. charoides* were first collected at a depth of –10 m CD in April 1998 and most of the plants were tetrasporic (97.5 % on 9-Apr) (Fig. 2.8). In the following growing season in December 1998, 30 % of the plants were tetrasporic and this percentage increased to 90 % on 22-Apr 1999. Majority of the plants remained vegetative in January and February in 1999.

2.3.3 Other observations

Among all the individuals of *Hypnea charoides* examined, presence of cystocarps and tetrasporangia on the same branch was occasionally observed. The first one was found in Lung Lok Shui on 3-May 1997 and another one among the drifted samples in A Ma Wan on 25-April 1998. This phenomenon was not common during the whole study period. Of hundreds of the plants observed, only two individuals were found to bear

both of these structures.

### 2.3.4 Environmental parameters

#### 2.3.4.1 Photoperiod

Mean monthly photoperiod in Hong Kong was calculated from the daily sunrise and sunset data obtained from the Hong Kong Observatory. From 1996 to 1999, the mean monthly photoperiod was recorded to be the longest in July (13.5:10.5h L:D) except in 1999 when the longest mean photoperiod was recorded in June (13.5:10.5h L:D), and the shortest in December (10.75:13.25h L:D) (Fig. 2.9). This seasonal variation appeared to be marked and steady without many fluctuations.

#### 2.3.4.2 Seawater temperature

Mean monthly water temperature was calculated as an average of all the temperatures recorded at 30 min interval within a month by the temperature probe. In A Ma Wan, the mean temperature of seawater at –1 to –2 m CD varied from a maximum of 29.5 °C in August 1998 to a minimum of 16.0 °C in February 1996 (Fig. 2.10). Slight fluctuations were observed during 1997 and the overall mean values were relatively lower than those of the other study years. In Lung Lok Shui, mean temperature at –2 to –3 m CD varied from a maximum of 29.7 °C in August 1998 to a minimum of 16.7 °C in February 1998 during the period from January 1998 to June 1999 (Fig. 2.11). While at –10 m CD measured from December 1998 to June 1999, seawater temperature decreased from 19.5 °C in December 1998 to a minimum of 17.9 °C in January and February in 1999 and rose to 26.7 °C in June 1999.

#### 2.3.4.3 Nutrient concentrations

Variations in the concentrations of ammonium ions, nitrates, nitrites and phosphates in

seawater samples collected from A Ma Wan and Lung Lok Shui during the study period (August 1996 to June 1999) are shown in Figs. 2.12 & 2.13 respectively. In A Ma Wan, concentrations of ammonium ions, nitrates and phosphates did not fluctuate (remained at a level below 1 μM) until November 1998, while throughout the whole sampling period, nitrite concentration remained steady, with values around or below 1 μM. (Fig. 2.12). Concentration of ammonium ions rose from 0.4 μM (29-Nov 1998) to a relatively higher level of 5.0 μM (24-Apr 1999) and a very sharp peak (21.5 μM) was recorded on 10-May 1999. Similarly, nitrate concentration increased from 1.0 μM (29-Nov 1998) to a level higher than 8.0 μM on 7-Feb and 21-Mar in 1999 and a sharp peak (22.3 μM) was also recorded on 10-May 1999. While for phosphates, concentration rose from 0.4 μM on 24-Sep 1998 to a level higher than 3 μM in the following months (November 1998 to April 1999) and a maximum of 5.1 μM was reached on 16-Jun in 1999.

Similar results were recorded in Lung Lok Shui, except that a sharp peak (14.5 μM) was observed in the concentration of nitrites on 6-Oct 1996 (Fig. 2.13). For all the other periods of sampling, nitrite concentration remained around or below 1 μM. For the other three nutrients, fluctuations occurred starting from November 1998. Concentrations of both ammonium ions and phosphates varied from 1 μM to 3 μM in 1999. While for nitrates, three peaks were recorded on 10-Jan (7.9 μM), 7-Feb (8.7 μM) and 30-May (10.8 μM) in 1999.

### 2.3.5 Statistical analysis

#### 2.3.5.1 A Ma Wan populations

In A Ma Wan, the mean length of *Hypnea charoides* was significantly negatively correlated with photoperiod ($r = -0.359$, $n = 38$, $p < 0.05$) and seawater temperature (r

= –0.669, n = 38, $p < 0.05$) but was not significantly correlated with any nutrient concentration in seawater (Table 2.1). No correlations were made in percentage occurrence of cystocarpic plants in –1 m CD attached samples with any physical parameters due to the small sample size. Percentage occurrence of tetrasporic plants in –1 m CD attached samples was significantly negatively correlated with photoperiod (r = –0.533, n = 24, $p < 0.05$) but positively correlated with seawater temperature (r = 0.635, n = 19, $p < 0.05$), while that of vegetative plants was negatively correlated with both photoperiod (r = –0.510, n = 24, $p < 0.05$) and seawater temperature (r = –0.635, n = 19, $p < 0.05$). Percentage occurrence of cystocarpic plants in attached and drifted samples at depths of –2 to –3 m CD was not correlated with any physical parameters. In attached samples, the percentage occurrence of tetrasporic plants showed a significant positive correlation with seawater temperature (r = 0.690, n = 13, $p < 0.05$) but that of vegetative plants, a negative correlation (r = –0.685, n = 13, $p < 0.05$). Similarly, a significant positive correlation was found in the percentage occurrence of tetrasporic plants of drifted samples with seawater temperature (r = 0.705, n = 17, $p < 0.05$) whereas a negative correlation was observed in that of vegetative plants (r = –0.689, n = 17, $p < 0.05$). No significant correlations were found in percentage occurrence of tetrasporic and vegetative plants with photoperiod and nutrient concentrations in both attached and drifted samples at –2 to –3 m CD.

2.3.5.2 Lung Lok Shui populations

In Lung Lok Shui, significant correlations with environmental parameters were only found in samples collected from the depth of –10 m CD. For these samples, the percentage occurrence of vegetative plants was significantly negatively correlated with both photoperiod (r = –0.553, n = 14, $p < 0.05$) and seawater temperature (r = –0.855, n = 8, $p < 0.05$) (Table 2.1).

## 2.4 Discussion

### 2.4.1 Seasonal occurrence and growth of *Hypnea charoides*

Annual growth of populations of *Hypnea charoides* in Ping Chau was initiated in early winter (November to December) and ended in late spring (April to May). These periods of time were when photoperiod and seawater temperature showed marked changes. Since photoperiod and temperature are environmental signals for seasonal change (Lüning 1990), it might be inferred that they are among the most important factors responsible for the seasonal growth of *H. charoides* in Ping Chau.

In fact, growth of many red algae was found to be particularly related to light (e.g. irradiance, photoperiod) and/or temperature, which served as a trigger for their seasonal behaviour (Burns & Mathieson 1972a, b, Kapraun 1978, Whittick 1978, Montalva & Santelices 1981, Friedlander & Zelikovitch 1984, Kain 1987, Schenkman 1989, Molenaar & Breeman 1994, Molenaar *et al.* 1996, Voskoboinikov *et al.* 1996, Hall & Murray 1998, see also Murray & Dixon 1992). In some cases, combined effects of different environmental parameters could facilitate the growth of marine algae. In a population of *Liagora californica* on Santa Catalina Island, longer photoperiods combined with warmer temperature enhanced branch growth and development (Hall & Murray 1998). In *Solieria chordalis*, growth response was governed by the combined effects of salinity and light at a given temperature (Brown 1995). In the latter case, growth rates were found to increase significantly with an addition of nitrogen, suggesting the influence of nutrients in seawater in algal growth.

High nutrient content of seawater is another ecological factor that favours algal growth in winter as marine algae start to consume their reserve materials for growth at this period of time (Lüning 1990). The effects of different nutrients (e.g. nitrates and

phosphates) on algal growth were documented in many studies in addition to the influences of light and temperature (Burns & Mathieson 1972b, Mathieson & Burns 1975, Kilar & Mathieson 1978, Brown 1995, Zinoun & Cosson 1996, Hurtado-Ponce & Pondevida 1997, Rabanal *et al.* 1997, Reani *et al.* 1998, see also Murray & Dixon 1992). Nonetheless, algal growth was not always favoured by high nutrient content. In *Gracilariopsis bailinae*, plants grew well with a low concentration of nutrients (Rabanal *et al.* 1997). While in some economic marine algae, like *Chondrus crispus* (Neish *et al.* 1977) and *Hypnea musciformis* (Guist *et al.* 1982), the carrageenan production of thalli increased by reducing nitrogen availability. Nitrogen in the form of ammonium ions was even toxic to *Solieria chordalis* at high concentrations (Brown 1995).

In the present study, the results obtained in A Ma Wan showed that annual growth of *H. charoides* was favoured by shorter photoperiod and lower seawater temperature. The initiation of this growth was more likely to be induced by change in seawater temperature rather than photoperiod (Table 2.1). This was more obvious in the shallow water samples in A Ma Wan, where growth of *H. charoides* was recorded in November 1996 when seawater temperature dropped from 28.2 °C (October 1996) to 24 °C (November 1996) and disappeared after May 1997 when seawater temperature rose from 24.5 °C (May 1997) to 26.7 °C (June 1997). This pattern was observed again in 1998, although a little bit late. Population of *H. charoides* appeared in December 1998 when seawater temperature dropped from 23.9 °C (November 1998) to 21.5 °C (December 1998) and disappeared after April 1999 when seawater temperature rose from 22.8 °C (April 1999) to 24.6 °C (May 1999). The pattern was less clear in 1997 when the temperature fluctuated more irregularly. Mean temperature lower than 24 °C was already recorded in October, but population of *H.*

*charoides* did not appear until January 1998. However, the population disappeared in May 1998, at a time when temperature rose from 23 °C in April to 27.1 °C in May. The lowest seawater temperature throughout the whole study period was 16 °C recorded in February 1996. It thus appears that population of *H. charoides* in A Ma Wan grows best within a temperature range from 16 °C to 24 °C regardless of the influences of other physical factors. Nonetheless, culture experiment is still needed to further investigate the relationship between growth of *H. charoides* and seawater temperature. In contrast, none of the physical parameters, including temperature, was significantly correlated with the growth of population of *H. charoides* at –1 to –2 m CD in Lung Lok Shui. This suggests that factors other than photoperiod, seawater temperature and nutrient concentrations were important in structuring its growth pattern. The role of seawater temperature in initiating the growth of Lung Lok Shui populations was probably less critical than that observed in A Ma Wan.

The apparent irregular growth pattern of *H. charoides* populations in Lung Lok Shui may be due to the much stronger wave action experienced by them. Stronger wave action caused fragmentation of the algal thalli. At Praia Vermelha, Brazil, higher abundance of vegetative plants of *Hypnea musciformis* was found at the time with a high wavelength and period of waves (Reis & Yoneshigue-Valentin 2000). In contrast, water movement resulted in a decrease of biomass in *Rhodymenia howeane* at La Herradura Bay, Chile (Vásquez *et al.* 1998). The latter implied that such condition could reduce the survivorship of algal plants (see also Rama Rao 1977, Schenkman 1989). Though in the present study, dramatic decrease of *H. charoides* biomass in Lung Lok Shui was not observed, wave action could have some influences on plant growth. Since the thalli of *H. charoides* can be broken apart easily, the action of strong waves resulted in various sizes of individuals. Hence, the influences of photoperiod,

seawater temperature as well as nutrient concentrations on the seasonal growth pattern were reduced. This would also explain why plants of *H. charoides* in Lung Lok Shui were found mostly entangled with *Sargassum* spp., which possess a strong holdfast for firm attachment, rather than being attached on the substratum directly.

The unusual sudden growth of *H. charoides* from July to November in 1998 also contributed to the irregular growth pattern of *H. charoide*s observed in Lung Lok Shui. Although the reason for the appearance of this growth period is unknown, the ability of *H. charoides* to survive and grow during summer months (i.e. longer photoperiod and warmer temperature) could not be ruled out. In some algal species, seasonal growth was not entirely controlled by physical factors alone but maybe due to endogenous regulations (Molenaar & Breeman 1994, 1997, Voskoboinikov *et al.* 1996, Makarov *et al.* 1999), allowing survival of these species under adverse conditions. Some tropical algae also exhibited no evident responses to environmental parameters (e.g. irradiance, temperature and salinity), indicating their natural ability to adapt to different marine conditions (Dawes *et al.* 1999). In a review of life history, reproduction and phenology of *Gracilaria*, Kain & Destombe (1995) found that there was no evidence of *Gracilaria* species anticipating the seasons by being triggered by a repeatable seasonal condition (e.g. photoperiod or water temperature) for optimal exploitation of predictable conditions. It seems that such species are responders (*sensu* Kain 1989) and they grow when they can, when the environment allows. For the populations of *H. charoides* in Lung Lok Shui, there might also be some endogenous regulations involved in their growth. Perhaps they are similar to some *Gracilaria* spp. that they grow whenever they can.

During this unusual, sudden growth period, *H. charoides* was observed to exhibit a

heterotrichous organization, i.e. its thallus was differentiated into a prostrate and an erect form. Members of the red algal order Gigartinales, to which *H. charoides* belongs, possess this categorization of thalli into two types of growth forms. An initial basal layer is first formed which then gives rise to filaments that form erect axes (Murray & Dixon 1992). In *Cryptopleura ramose* or *Plocamium cartilagineum*, the realized developmental pathway for their particular mode of erect or prostrate growth appeared to be correlated with irradiance (Dixon 1973). Though factors that induce *H. charoides* to exhibit heterotrichy are not known, it appears that heterotrichy could be a means of increasing the opportunities to successfully perennate its thallus throughout any open space (Murray & Dixon 1992, see also Chapter 3).

### 2.4.2 Reproductive seasonality

Effects of seawater temperature on phenology of marine algae have been well documented in the past (Adey 1973, Mathieson & Burns 1975, De Wreede 1976, Kapraun 1978, Whittick 1978, Prince & O'Neal 1979, Luxoro & Santelices 1989, Schenkman 1989, Narasimha Rao 1995, Voskoboinikov *et al.* 1996). Although in some cases, water temperature *per se* does not directly affect algal reproduction, it may initiate the reproduction events in conjunction with other environmental parameters like irradiance/photoperiod (Kapraun 1978, Prince & O'Neal 1979) and/or nutrient concentrations (Reed *et al.* 1996, Stimson *et al.* 1996, Rabanal *et al.* 1997). In some red algal species, photoperiod and seawater temperature were found to be particularly important to reproductive events among many environmental factors (Molenaar & Breeman 1994, Molenaar *et al.* 1996, Zamorano & Westermeier 1996, Hall & Murray 1998). In the present study, variations in photoperiod and seawater temperature seemed to play a more important role in controlling the occurrence of reproductive plants in the population of *H. charoides* in A Ma Wan than that in Lung Lok Shui. It

was more obvious in the attached samples collected at –1 m CD in A Ma Wan, in which shorter photoperiod and higher temperature were more favourable for the growth of tetrasporic plants. Besides, percentage occurrence of tetrasporic plants in attached and drifted samples at depths of –2 to –3m CD was also enhanced by higher temperature, indicating that increasing seawater temperature may favour tetrasporogenesis in the populations of *H. charoides* in A Ma Wan. Induction of tetrasporogenesis was also reported in other red algal species, like *Coelothrix irregularis* and *Dictyopteris delicatula* (Pakker *et al.* 1995). In a population of *Gracilaria heteroclada* in Central Philippines, a positive correlation (r = 0.6586) was also obtained in the percentage occurrence of tetrasporophytes with seawater temperature (Luhan 1996). A sudden rise in water temperature (+ 5 °C) together with a decrease of incident light could even trigger a massive tetraspore release in *Gracilaria bursa-pastoris* (Marinho-Soriano *et al.* 1998). The onset and end of the growth and reproductive seasons may also be triggered by many factors other than temperature (Dring 1974, Lobban & Harrison 1994). Nevertheless, none of the other environmental parameters investigated appeared to induce development of reproductive plants in both A Ma Wan and Lung Lok Shui.

Throughout the whole study period, cystocarpic plants were very rare among all groups of samples and were even absent in Lung Lok Shui. This implies that the populations of *H. charoides* in Ping Chau were dominated by vegetative and tetrasporic plants. Natural populations do not always have equal proportions of isomorphic generations. Although it was evident that the gametophytic:sporophytic ratio of fronds in populations of *Chondrus crispus* in sublittoral Prince Edward Island of Canada was a result of stochastic events, with both generations having equal chances of becoming established (Laura Lazo *et al.* 1989), cystocarpic plants of the

same species were found to be relatively more common and abundant than tetrasporic plants in other places (Mathieson & Burns 1975). Piriz (1996) observed clear predominance of cystocarpic plants in the population of *Gigartina skottsbergii* in Argentina, suggesting that there were differential adaptive strategies for each growth phase in its life cycle. Predominance of gametophytes was also reported in other red algae, like *Iridaea cordata* (May 1986), *Iridaea laminarioides* (Luxoro & Santelices 1989) and *Mazzaella cornucopiae* (Scrosati 1998). On the contrary, the rarity of gametophytes and/or the predominance of tetrasporophytes were even more commonly documented in many other red algal species (Hansen & Doyle 1976, Rama Rao 1977, Hoyle 1978, Kilar & Mathieson 1978, Whittick 1978, Kaliaperumal & Umamaheswara Rao 1982, Schenkman 1989, Narasimha Rao 1995, Vásquez *et al.* 1998, Cecere *et al.* 2000, Reis & Yoneshigue-Valentin 2000).

Absence of male plants and rare occurrence of female ones in *Hypnea* species were also observed in places like India (Rama Rao 1977) and Brazil (Schenkman 1989, Reis & Yoneshigue-Valentin 2000). Two questions were raised by Schenkman (1989): (1) Why are fertile gametophytes rare despite the high production of tetraspores in several genera of Rhodophyta? (2) Is it due to the apomeiotic division of the sporangia or to a greater ability of diploid plants to propagate vegetatively compared to the haploid phase, or neither?

There are several explanations to the first question. Cecere *et al.* (2000) stated that gametophytes, which were ephemeral, might die back soon after reproduction or might become reproductive when they were still so small to be underestimated (see also Breeman *et al.* 1988). Similarly, Reis & Yoneshigue-Valentin (2000) thought that male plants of most red algae were rarely recorded probably because they manifested

themselves during a very short period of time or it was a bit difficult to recognize them. While Mathieson (1989) explained that relatively longer lifespan of tetrasporophytes in wild populations allowed them to produce more upright thalli per plant and thus they became more robust under stressful conditions. In a culture study of *Stictosiphonia hookeri* from different localities, West *et al.* (1996) suggested two possibilities to explain the low frequency of gametophytes: (1) tetraspores do not survive germination due to their low viability, thus survival and dispersal are probably achieved by vegetative growth and fragmentation (see also Hansen & Doyle 1976 and Cecere *et al.* 2000), (2) gametophytes reproduce and die more quickly than tetrasporophytes. All these would lead to rare occurrence of gametophytes and a prevalence of tetrasporophytes (see also Rama Rao 1977).

For the second question, both suggestions are possible. Variation in gametophyte-to-sporophyte ratios could be attributable to greater fecundity and survivorship (relative fitness) of one phase or to asexual phenomena, such as vegetative propagation and/or apomixis (see Hawkes 1990). In algae, apomixis can occur via apogamy/parthenogenesis or apomeiosis. Since in red algae, vegetative reproduction is a widespread and important strategy in maintaining their populations, many of them are able to develop apomeiotic tetrasporangia, resulting in a life history where new tetrasporophytes develop directly from tetraspores (Hansen & Doyle 1976, Rama Rao 1977, Hoyle 1978, Magne 1987, see also Hawkes 1990 and Murray & Dixon 1992). Hence, the phenomenon showing high frequency of tetrasporophytes in certain species of the family Hypneaceae suggested that the principal reproductive mode could be resulted from apomeiosis (West & Hommersand 1981). Nevertheless, Schenkman (1989) believed that the *Hypnea* population studied in Brazil maintained itself mainly by vegetative reproduction rather than apomeiosis as normal meiosis was observed in

the tetrasporangia in a previous study (Schenkman 1986).

Since *Hypnea* spp. exhibit isomorphic life cycles, the many vegetative plants of *H. charoides* observed in Ping Chau during the growing seasons could be either infertile gametophytes or tetrasporophytes. If the suggestions previously mentioned above, that gametophytes might die soon after reproduction (Cecere *et al.* 2000) or they manifested themselves only during a very short period of time (Reis & Yoneshigue-Valentin 2000), are applicable to populations of *H. charoides* in Ping Chau, the processes from fertilization of gametes to the development of carposporophytes and from carpospores to tetrasporophytes should be relatively short. This leads to the rare occurrence of cystocarpic plants. The tetrasporophytes became fertile and released tetraspores at the end of the growing season. These tetraspores persisted in summer months and then gave rise to gametophytes in the next growing season, completing the life cycles. However, the viability of free-floating spores is exceedingly low and this is true for tetraspores (Santelices 1990, Lobban & Harrison 1994). Then, how could they survive in summer? Hoffmann & Santelices (1991) suggested that this role could be fulfilled by developing into microscopic forms that remained in a state of suspended growth. Some algal species existed as a microthallus or prostrate disc-like phase in order to survive adverse conditions like intense high summer temperatures and ice scour (Schoschina *et al.* 1996). In *Acanthophora najadiformis* populations in the Ionian Sea, Cecere *et al.* (2000) explained that propagules were substituting for tetraspores which were not viable and they acted either as perennating organs or resting organs to overcome unfavourable environmental conditions. Such kind of (asexual) propagules were found to have substantially more nutrient reserves and greater photosynthetic potential than spores (Cruz Adames & Ballantine 1996). Hence, it is possible that tetraspores of *H. charoides* in Ping Chau are able to develop and exist

in a form (e.g. sporelings or propagules) that can survive in the water column during summer and then grow into adult plants when the conditions are optimal (i.e. winter) (see discussion in Chapter 3).

Despite the low percentage occurrence of reproductive plants in populations of *H. charoides* in A Ma Wan during the whole study period, the frequency of observing cystocarpic (among drifted samples) and tetrasporic (–1 m CD, –2 to –3 m CD and drifted samples) plants in Lung Lok Shui populations was relatively higher in 1999. There are several possibilities: (1) the process from fertilization of gametes to the development of tetrasporophytes was prolonged, increasing the chances of observing cystocarpic plants; (2) the tetraspores produced in the previous growing season in 1998 might undergo apomeiosis and develop into a tetrasporophyte; (3) the ripening of tetrasporangia was premature. These observed phenomena might be a response to stressful environment conditions (e.g. severe fluctuations of nutrient concentrations in seawater in 1999). The real reasons, however, could not be determined at present.

Population recruitment of *H. charoides* during the growing season was thought to be provided by vegetative fragmentation as the timing of occurrence and reproduction were similar among different groups of samples (–1 m CD, –2 to –3 m CD, –5 m CD and drifted samples) in A Ma Wan. Many drifted samples were found at the beginning of the growing season, suggesting that tetraspores (or other forms developed from them) produced at the end of the previous season might grow into a drifted plant living in the water column and/or that the loosely attached individuals could easily disperse itself (or branches) in order to populate the whole area. The stability of this free-floating population ensured the vegetative fragmentation as an effective means of population recruitment of *H. charoides* in A Ma Wan (see Perrone & Cecere 1997).

Without considering the unusual, sudden growth of *H. charoides* in 1998, similar pattern of vegetative fragmentation and population recruitment would likely be occurring among the samples collected at depths of –1 to –2 m CD and –10 m CD in Lung Lok Shui. This process of population recruitment is more likely to happen in Lung Lok Shui as indicated by the fact that thalli of *H. charoides* were mostly found entangled with *Sargassum* spp. rather than loosely attached on the substratum. Furthermore, this might be an adaptation to populate a place with strong wave action. The relatively high abundance of tetrasporic plants in Lung Lok Shui could also be another adaptation of *H. charoides* to survive there as tetrasporophytes could be more resistant to hydrodynamic forces (Scrosati 1998). In addition, the high abundance of tetrasporic plants observed in 1998 (100 % in October) during the unusual growth period might be the result of selective forces acting in different ways on the different phases, with one phase being better adapted than the other (Zamorano & Westmeier 1996, Reis & Yoneshigue-Valentin 2000). It could also be a response of *H. charoides* populations to some undetected changes in the surroundings. As Lobban and Harrison (1994) stated, selection will favor rapid growth, early reproduction, and short life spans in unstable areas. Among algae, different types of stress induce different physiological responses and there may have different ecological outcomes (Davison & Pearson 1996).

The onset of reproduction coinciding with the end of the growth phase has been recorded in several red algal species (Burns and Mathieson 1972, Kilar & Mathieson 1978, Kain & Norton 1990, Voskoboinikov *et al.* 1996, Molenaar & Breeman 1997). In this study, populations of *H. charoides* in A Ma Wan became tetrasporic when the growing season came to the end. This could be advantageous as there would be more free substrata due to the mortality of many other marine algae during this period (Kim

& De Wreede 1996, Scrosati 1998, see also discussion in Chapter 3). Another possible reason was that energy within the plant was directed toward reproduction instead of growth. Therefore, although seasonal growth of *H. charoides* in A Ma Wan was a response to variations in seawater temperature, its cessation in April/May might be a result of the transfer of energy into reproduction. However, this explanation is not always true for all algal populations. Voskoboinikov *et al.* (1996) noted that *Phycodrys rubens* previously recorded in other places also stopped growing in early summer but the main reproductive peak did not occur until late winter to early spring. Molenaar & Breeman (1997) also found no evidence for a trade-off between growth and reproduction in populations of *Delesseria sanguinea*, *Membranoptera alata* and *Phycodrys rubens* in both Helgoland, Germany, and Roscoff, France. They all concluded that there was no direct antagonistic effect between growth and reproduction, each being regulated by different environmental factors and/or endogenous circannual rhythm. Nonetheless, population of *H. charoides* in Lung Lok Shui was able to survive during summer, indicating that an endogenous regulation was possibly involved.

### 2.4.3 Occurrence of cystocarps and tetrasporangia on the same thallus in *Hypnea charoides*

During the examination of reproductive structures in *H. charoides*, presence of cystocarps and tetrasporangia on the same branch was observed twice (25-April 1998 in A Ma Wan and 3-May 1997 in Lung Lok Shui). Abnormal pairing of these two reproductive organs had been recorded in certain red algae, like *Cystoclonium purpureum* (Gigartinales), *Chondria baileyana* (Ceramiales) (Edelstein *et al.* 1974), *Polysiphonia harlandii* (Cheung *et al.* 1984) and many *Gracilaria* species (see Kain and Destombe 1995). Plants can bear both structures either on separate parts of the

thallus or on the same. Explanations, suggested by Kain & Destombe (1995), include the *in situ* germination of tetraspores (enabling gametophytes to develop as epiphytes on parental tetrasporophytes), the coalescence of spores or basal discs arising from spores to form a chimaera, mitotic recombination during cell division (resulting in occurrence of diploid male and female cells on the same tetrasporophyte), a natural mutation during which female expression is repressed, allowing the formation of carpogonia on male plants which thus became bisexual, and finally, incomplete formation of cross-walls in tetrasporangia (Kain & Destombe 1995). Though it is not clear which explanation(s) would be more applicable to the populations of *H. charoides* in Ping Chau at the moment, this could be a strategy for the tetraspores to survive and germinate. The percentage occurrence of cystocarpic plants in both A Ma Wan and Lung Lok Shui could also be underestimated. This phenomenon of having both gametangial and non-gametangial sexual reproductive structures on a single thallus was not commonly recorded in Hong Kong (see Cheung *et al.* 1984). The present finding is thus a first record for *H. charoides* in Hong Kong.

Table 2.1. Correlation of mean length and percentage occurrence of plants with different reproductive phases of *Hypnea charoides* with different environmental parameters (photoperiod, seawater temperature, concentrations of ammonium ions, nitrites, nitrates and phosphates) in A Ma Wan (AMW) and Lung Lok Shui (LLS). Each value represents the Pearson Product Moment Correlation coefficient "r". Sample size is shown in ( ). Significant correlation ($p < 0.05$) is indicated by an asterisk (*). "NA" represents "Not applicable".

| Site | | Variables | Photoperiod | Temperature | $NH_4$ | $NO_2$ | $NO_3$ | $PO_4$ |
|---|---|---|---|---|---|---|---|---|
| AMW | | Mean length (cm) | –0.359* (38) | –0.669* (38) | 0.323 (18) | 0.283 (19) | 0.461 (17) | 0.362 (18) |
| | –1 m CD | Tetrasporic (%) | –0.533* (24) | 0.635* (19) | 0.186 (10) | –0.506 (11) | 0.038 (9) | 0.237 (9) |
| | | Vegetative (%) | –0.510* (24) | –0.635* (19) | –0.186 (10) | 0.506 (11) | –0.038 (9) | –0.237 (9) |
| | –2 to –3 m CD | Cystocarpic (%) | 0.207 (15) | 0.389 (13) | NA | NA | NA | NA |
| | | Tetrasporic (%) | 0.364 (15) | 0.690* (13) | –0.148 (7) | –0.481 (7) | –0.022 (6) | 0.187 (7) |
| | | Vegetative (%) | –0.363 (15) | –0.685* (13) | 0.148 (7) | 0.481 (6) | 0.022 (7) | –0.187 (7) |
| | Drifted | Cystocarpic (%) | –0.277 (19) | 0.187 (17) | 0.115 (7) | –0.425 (7) | 0.524 (6) | 0.513 (7) |
| | | Tetrasporic (%) | 0.334 (19) | 0.705* (17) | –0.070 (7) | –0.496 (7) | 0.309 (6) | 0.263 (7) |
| | | Vegetative (%) | –0.284 (19) | –0.689* (17) | 0.045 (7) | 0.501 (7) | –0.352 (6) | –0.307 (7) |
| LLS | | Mean length (cm) | –0.068 (33) | –0.224 (12) | 0.506 (14) | 0.142 (16) | –0.030 (15) | –0.004 (14) |
| | –1 m CD | Tetrasporic (%) | 0.275 (22) | 0.552 (11) | –0.107 (7) | –0.399 (8) | –0.201 (8) | –0.360 (7) |
| | | Vegetative (%) | –0.275 (22) | –0.552 (11) | 0.107 (7) | 0.399 (8) | 0.201 (8) | 0.360 (7) |
| | –10 m CD | Tetrasporic (%) | 0.049 (14) | –0.013 (8) | NA | NA | NA | NA |
| | | Vegetative (%) | –0.553* (14) | –0.855* (8) | NA | NA | NA | NA |

Fig. 2.1. Variation in mean length (cm ± SD) of *Hypnea charoides* (n = 100) at –1 to –2 m CD in A Ma Wan from January 1997 to June 1999.

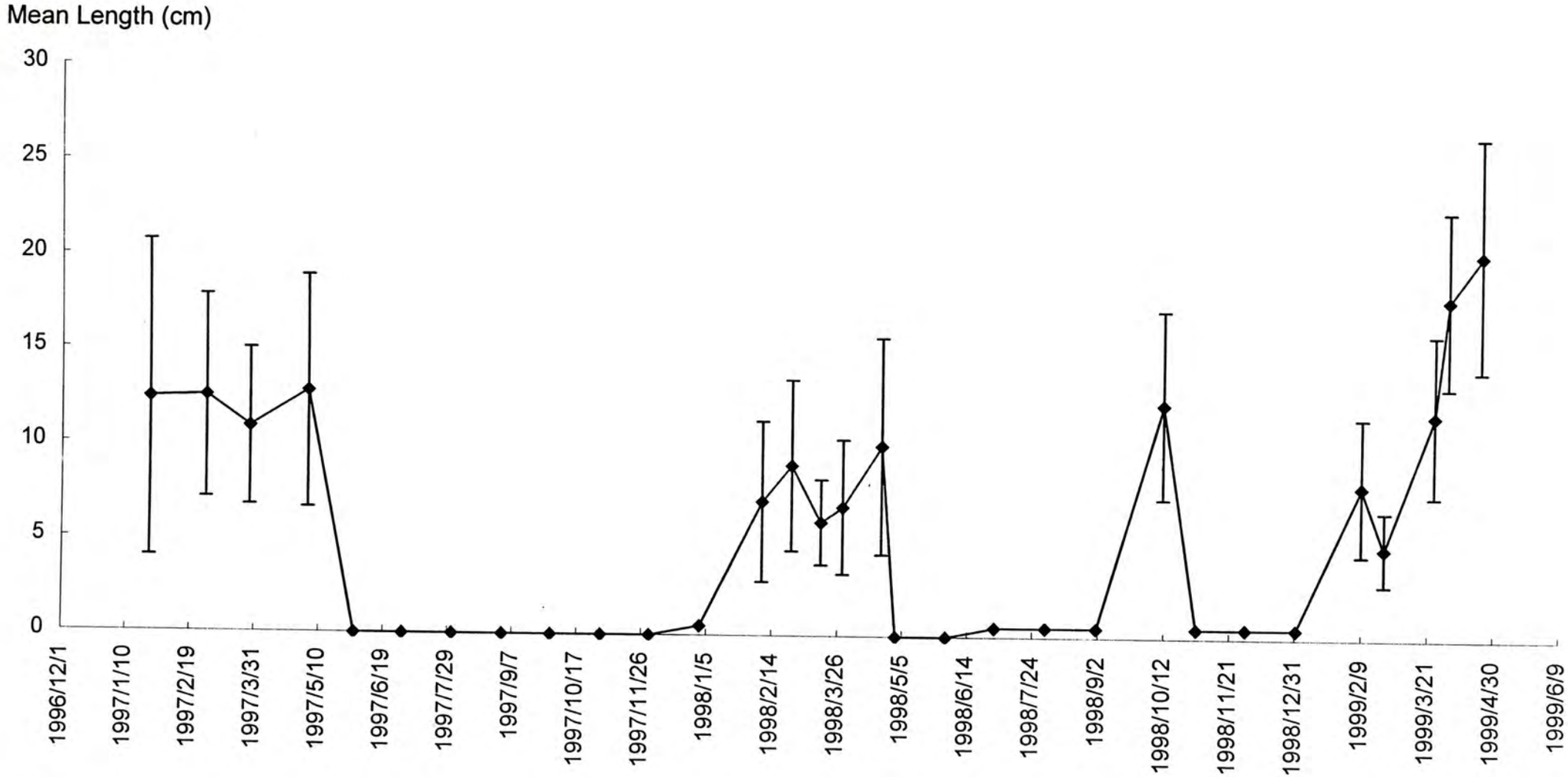


Fig. 2.2. Variation in mean length (cm ± SD) of *Hypnea charoides* (n = 100) at –1 to –2 m CD in Lung Lok Shui from January 1997 to June 1999.

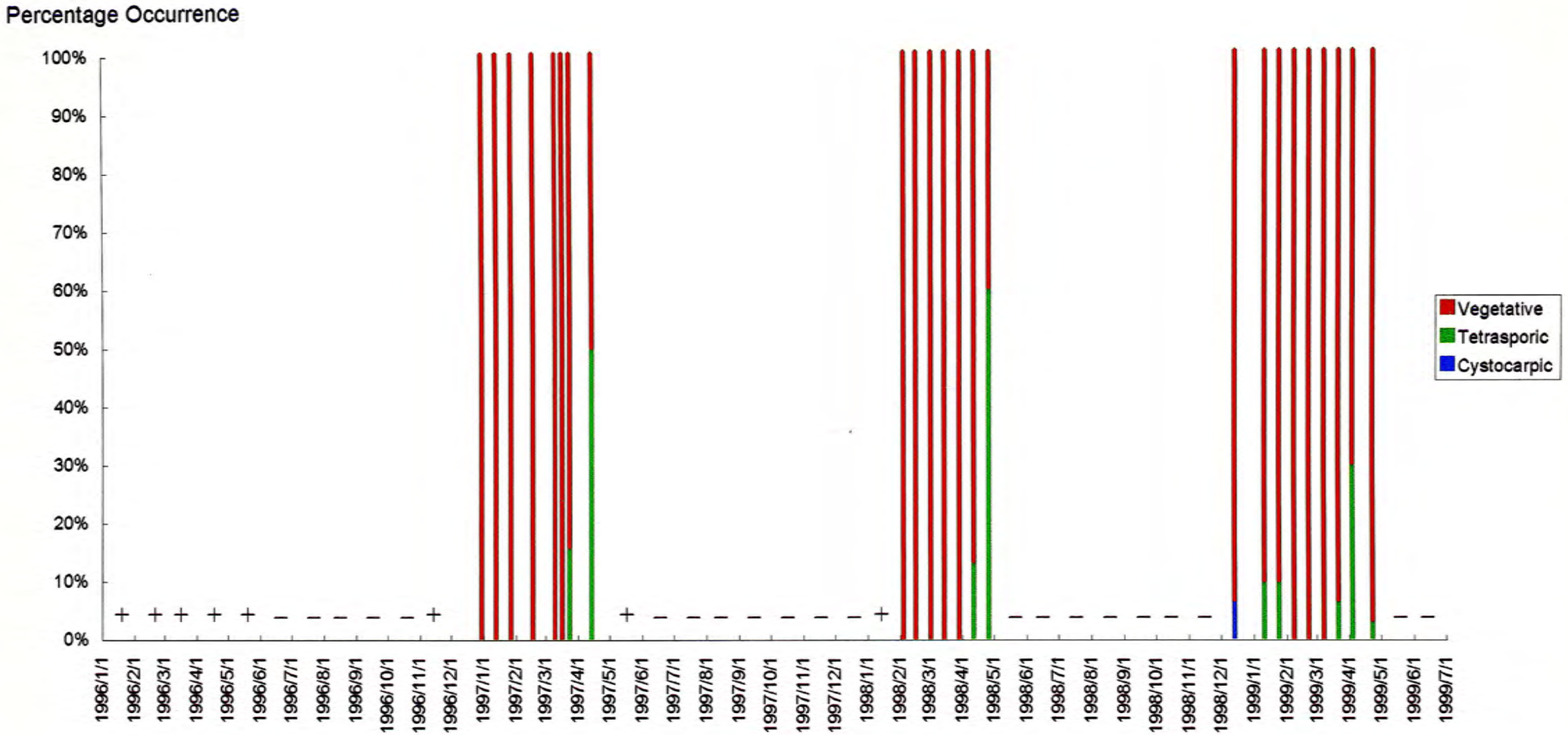


Fig. 2.3. Seasonal occurrence and percentage of reproductive phases in attached population of *Hypnea charoides* (n = 30) at −1 m CD in A Ma Wan from January 1996 to June 1999 ("+" – plants were present; "–" – plants were absent).

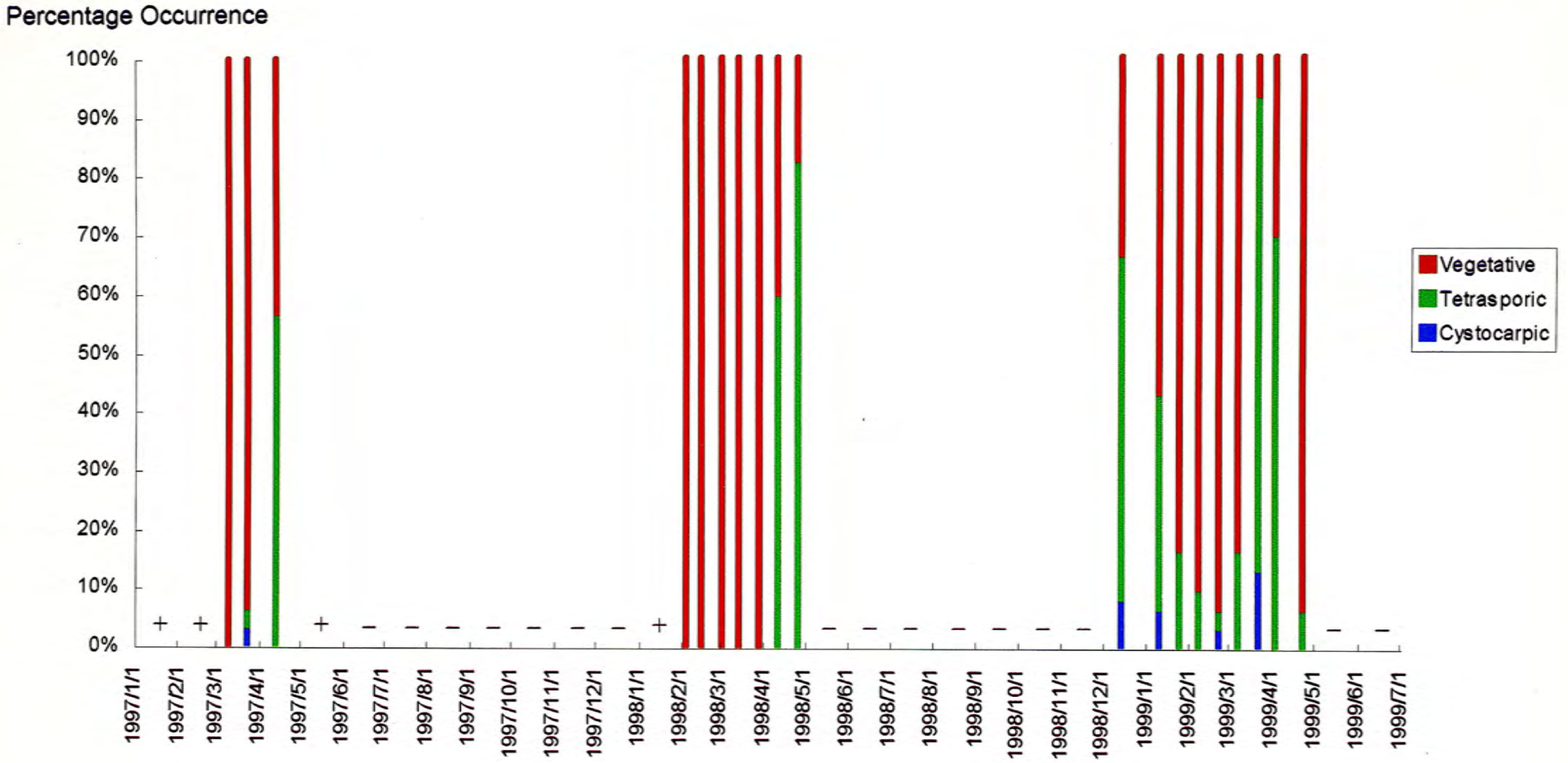


Fig. 2.4. Seasonal occurrence and percentage of reproductive phases in drifted population of *Hypnea charoides* (n = 30) at –2 to –3 m CD in A Ma Wan from January 1997 to June 1999 ("+" – plants were present; "–" – plants were absent).

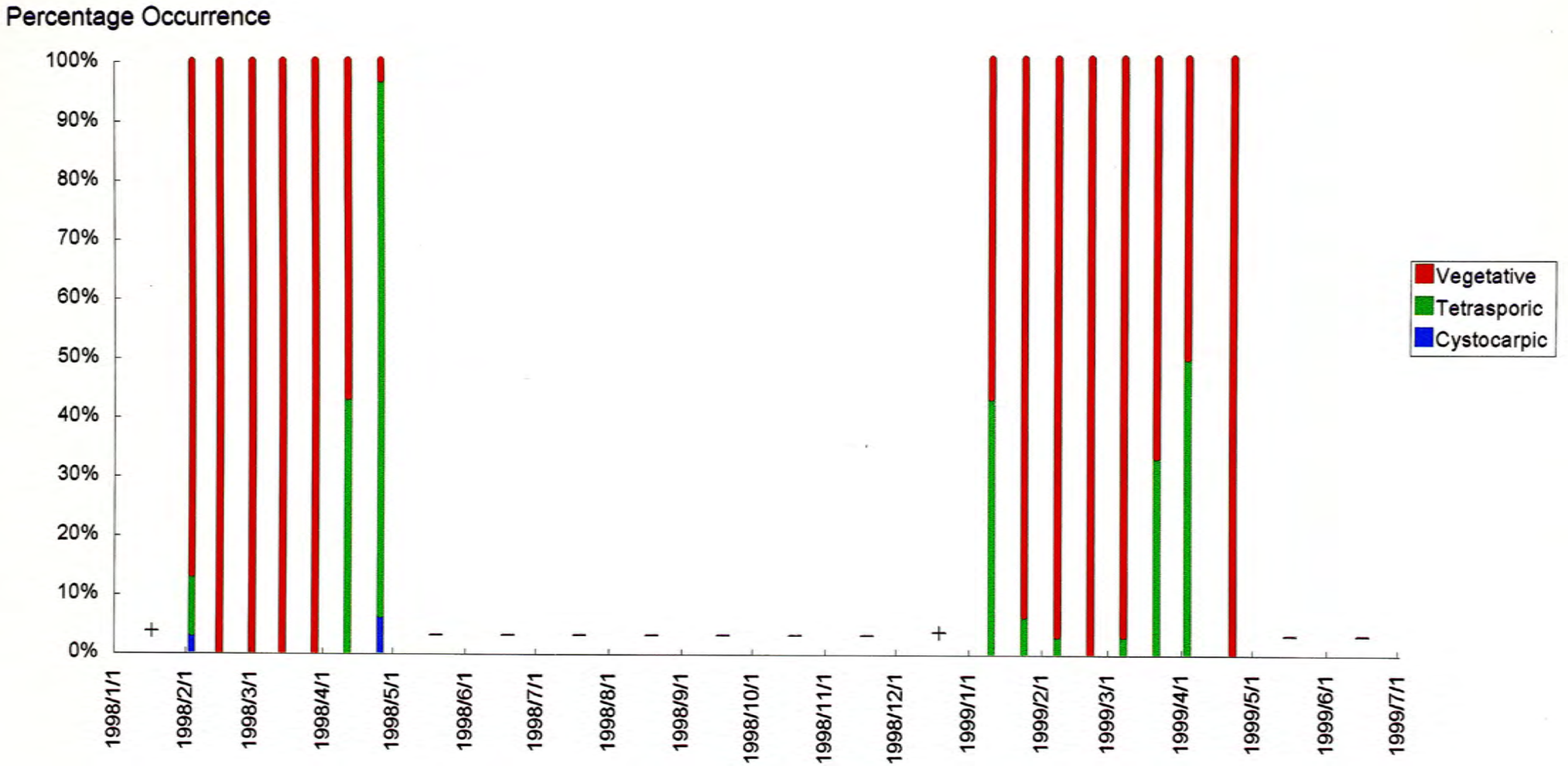


Fig. 2.5. Seasonal occurrence and percentage of reproductive phases in attached population of *Hypnea charoides* (n = 30) at –2 to –3 m CD in A Ma Wan from January 1998 to June 1999 ("+" – plants were present; "–" – plants were absent).

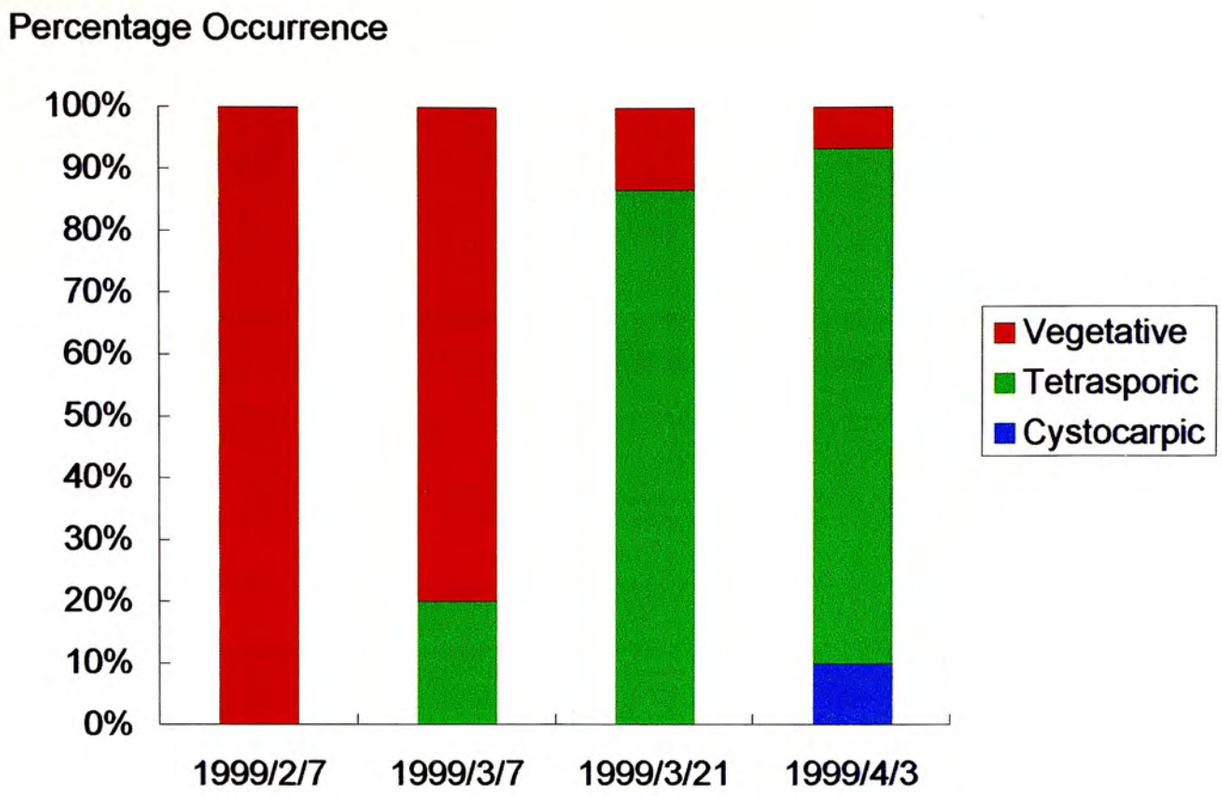


Fig. 2.6. Seasonal occurrence and percentage of reproductive phases in population of *Hypnea charoides* at –5 m CD in A Ma Wan from February to April 1999.

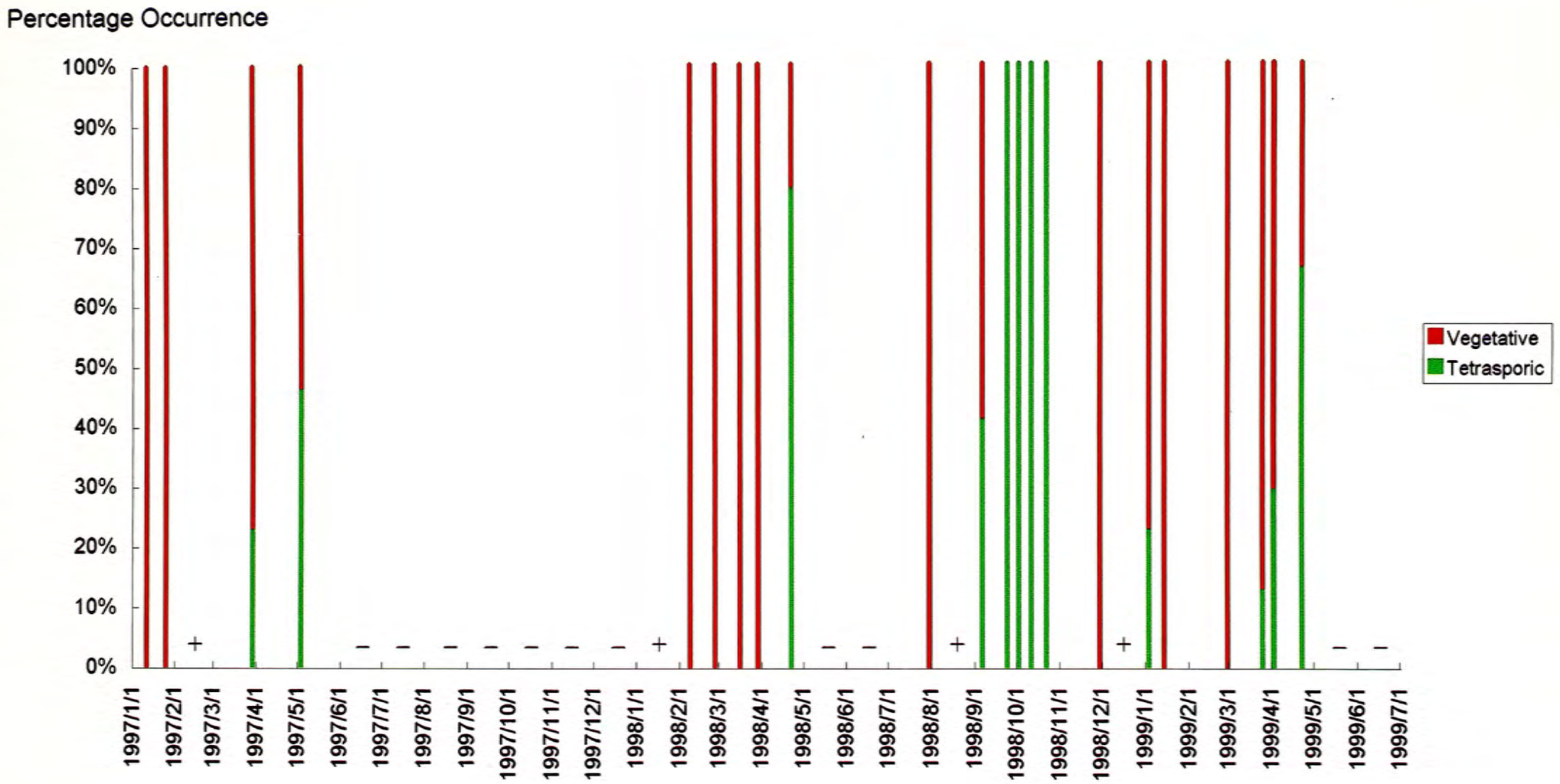


Fig. 2.7. Seasonal occurrence and percentage of reproductive phases in population of *Hypnea charoides* (n = 30) at –1 to –2 m CD in Lung Lok Shui from January 1997 to June 1999 ("+" – plants were present; "–" – plants were absent).

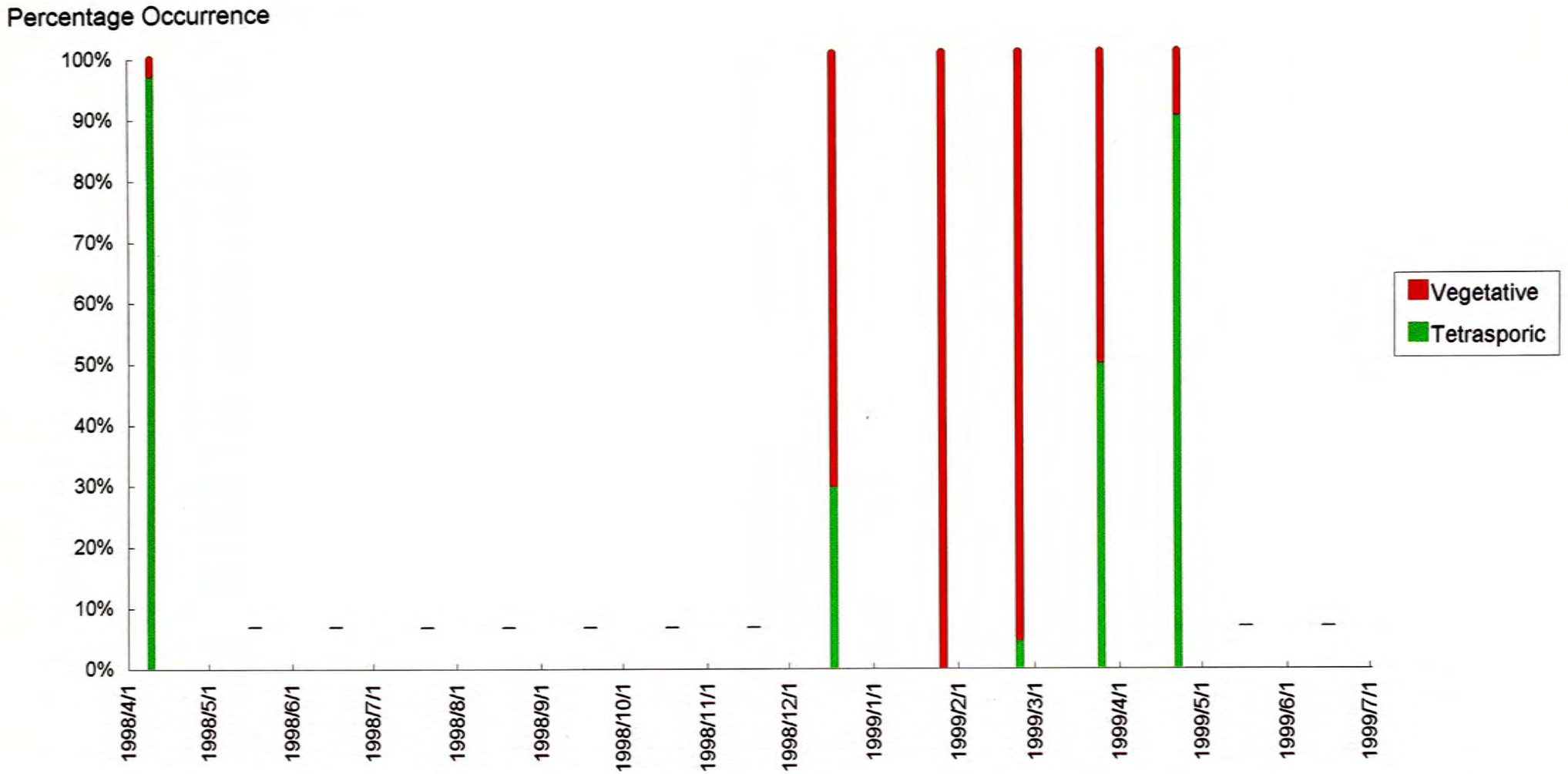


Fig. 2.8. Seasonal occurrence and percentage of reproductive phases in population of *Hypnea charoides* (n = 30) at −10 m CD in Lung Lok Shui from April 1998 to June 1999 ("+" – plants were present; "–" – plants were absent).

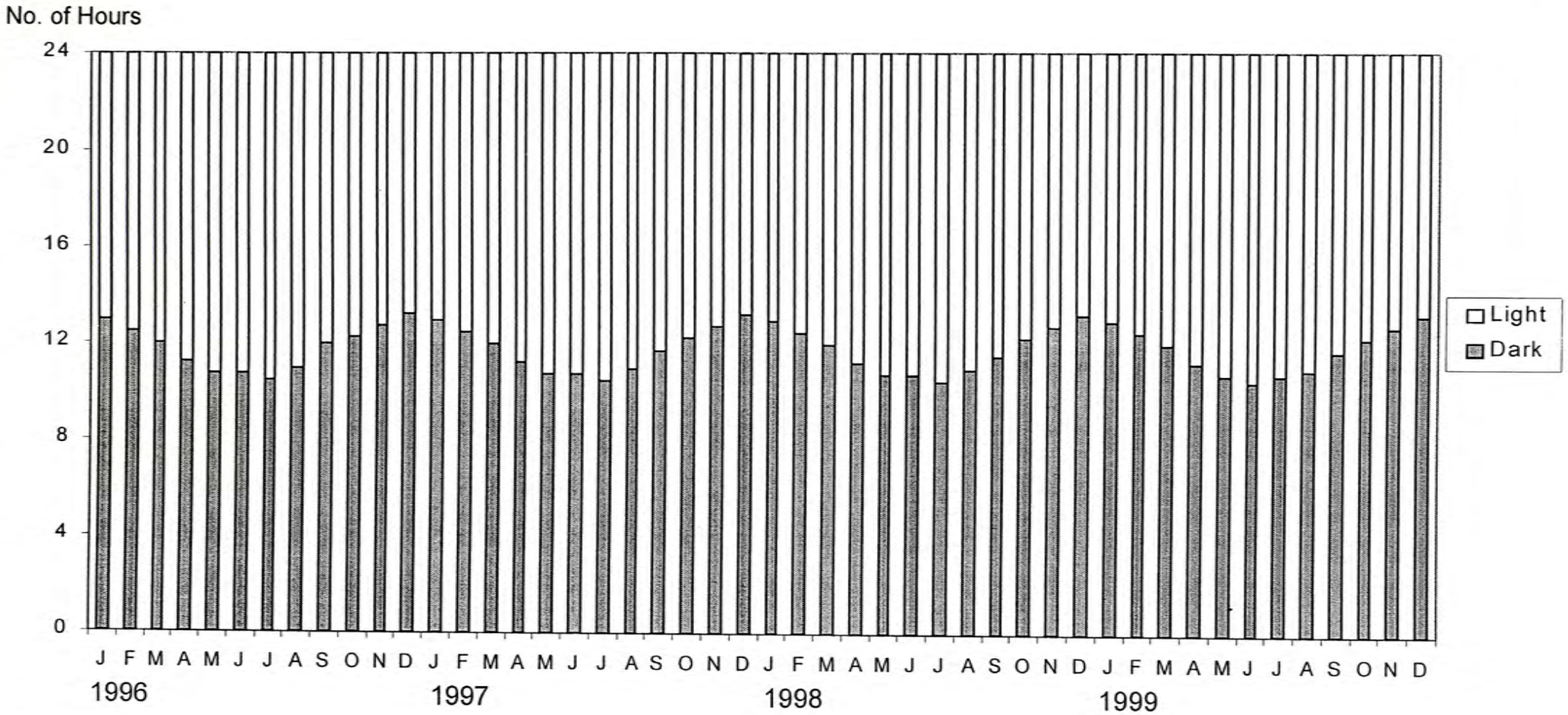


Fig. 2.9. Mean monthly variation in photoperiod (number of hours of daylight vs dark) recorded in Hong Kong from January 1996 to December 1999 (from Hong Kong Observatory).

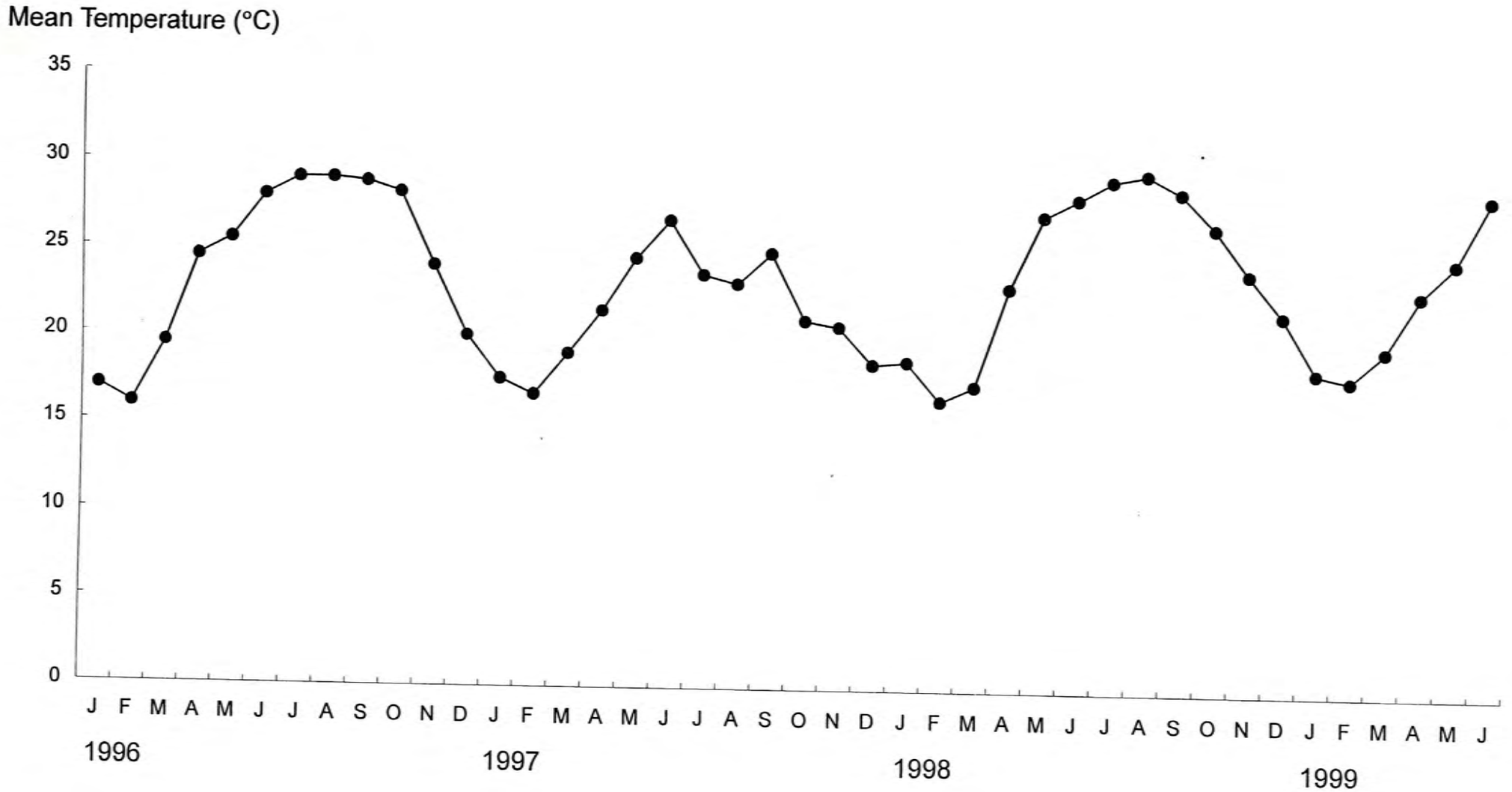


Fig. 2.10. Mean monthly variation in seawater temperature (°C) recorded at depth of –1 to –2 m CD in A Ma Wan from January 1996 to June 1999. Standard deviations are not shown.

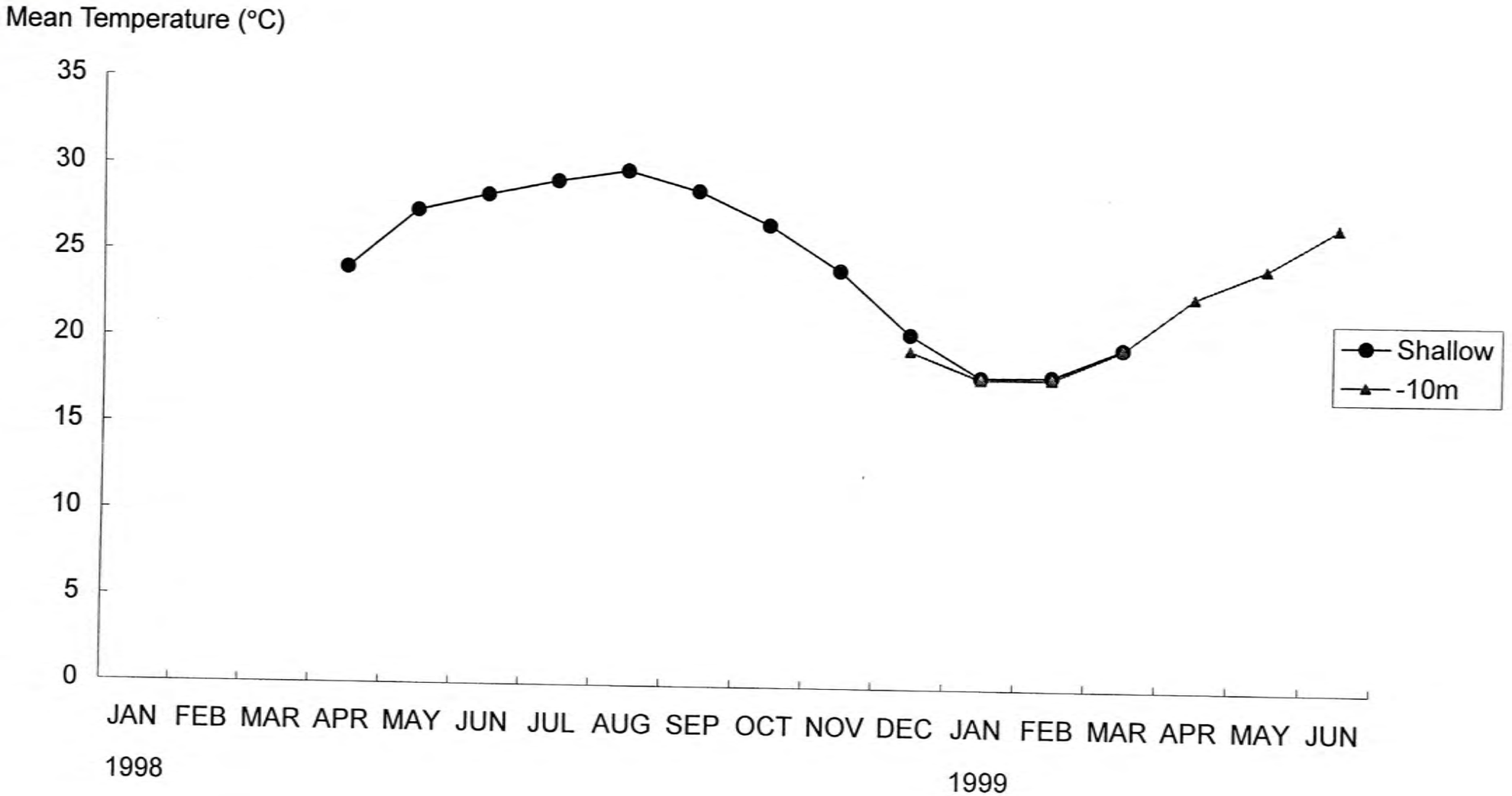


Fig. 2.11. Mean monthly variation in seawater temperature (°C) recorded in shallow water and at –10 m CD in Lung Lok Shui from January 1998 to June 1999. Standard deviations are not shown.

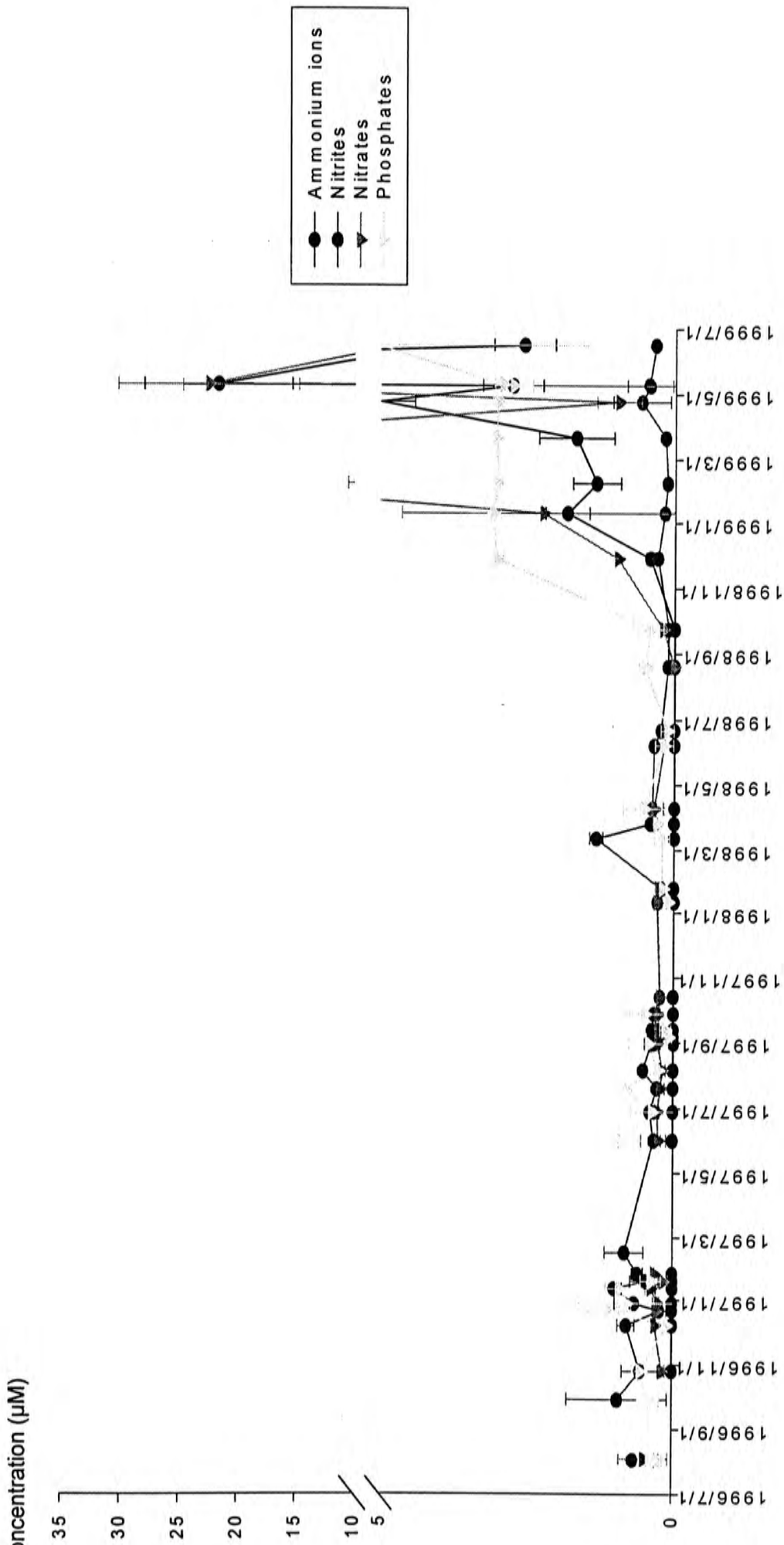


Fig. 2.12. Variation in concentrations of different nutrients (µM) in seawater recorded in A Ma Wan from August 1996 to June 1999.

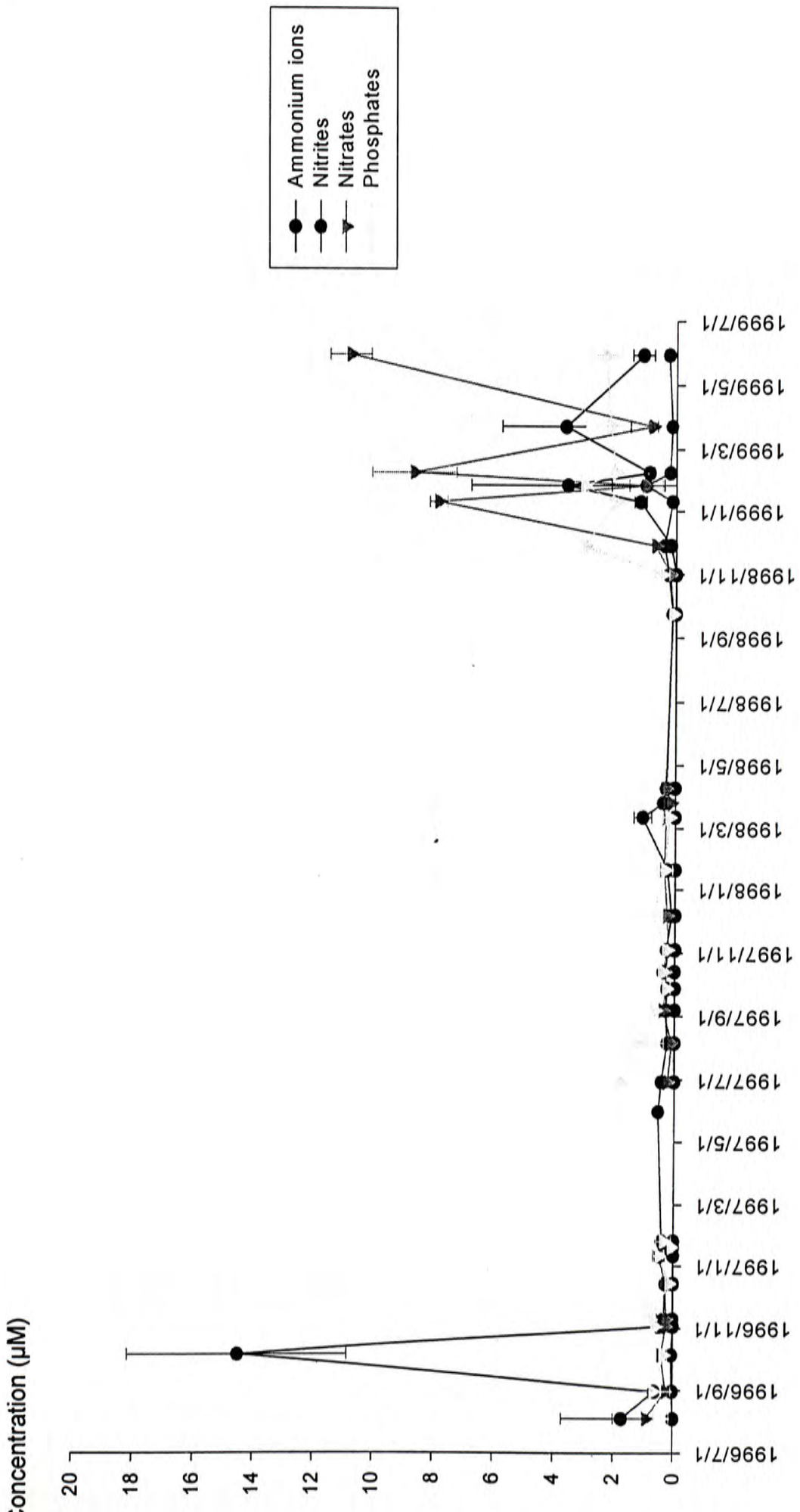


Fig. 2.13. Variation in concentrations of different nutrients (µM) in seawater recorded in Lung Lok Shui from August 1996 to June 1999.

# Chapter 3

# Algal Recruitment on Artificial Clearings

## 3.1 Introduction

Dayton (1971) suggested that sessile organisms have in common two resource pools: (1) the primary space, the substratum on which they attach, and (2) the aquatic milieu around them, which is the source of their physical, organic and inorganic nutrients. For marine benthic algae, space is limiting. Among banks of microscopic forms, competition for space can be very great, even greater than that in seed plants (Hoffmann & Santelices 1991). In addition to this, competition for space can be hierarchical, i.e. the species can be ranked with respect to their ability to overgrow one another (Dayton 1971, Roughgarden *et al.* 1988). So, it raises a question commonly asked by many marine ecologists: Who will be the first/last/dominant colonist(s)?

In natural environments, patches of open space can be generated by various physical disturbances like removal of algae by severe storms (Underwood 1998) or violent perturbations (Airoldi 2000), removal of sessile invertebrates (e.g. mussels) by log damage or winter storm waves (Dayton 1971, Sousa 1984, Blanchette 1996), and overturning of boulders by wave action (Sousa 1979a, b). Large-scale episodic events such as El Niños, La Niñas or rare storms exert considerable impacts (Dayton *et al.* 1992). Sizes of patches generated by these events strongly affect the subsequent community dynamics. In a rocky intertidal algal community in southern California, the resultant patterns of recolonization on the cleared patches and the mechanisms of change in species composition depended in part on the size of the initial clearing and on whether adult plants were present around the opening or not (Sousa 1979b). Patch size also strongly influenced algal succession within experimental clearings in mussel

beds by affecting the abundance of grazers which determined algal recruitment success (Sousa 1984). In a midlittoral community on the west coast of Italy (Ligurian Sea), patch size significantly affected species recovery in which macroalgae were more abundant in the large gaps than in the small ones (Benedetti-Cecchi & Cinelli 1993). Rate of recolonization in the Transkei region of southern Africa was also directly related to gap size, with the smallest gaps remaining relatively free of algae and the largest ones showing greatest recovery after 12 months (Dye 1993).

By far, however, studies on natural gap formation and algal recolonization are limited. More information on algal recruitment has been generated from studies that made use of artificial clearings on natural substrata (Dayton 1972, Hansen 1977, Sousa 1979b, 1984, Dayton *et al.* 1984, 1992, Ang 1985, Kennelly 1987, Stewart 1989, Benedetti-Cecchi & Cinelli 1993, Dye 1993, Blanchette 1996, van Tamelen & Stekoll 1996, Kim 1997, Underwood 1998, Jenkins *et al.* 1999, Airoldi 2000). In some studies, different types of treatments were applied on the clearing areas so as to compare different patterns of recruitment (Kennelly 1987, Stewart 1989, Blanchette 1996, Underwood 1998). For example, in order to test the effects of turf on the recruitment of *Ecklonia radiata* and understorey species, Kennelly (1987) carried out four treatments in the experimental areas: (1) three areas dominated by turf algae were cleared of turf, exposing the underlying encrusting algae; (2) three similar areas were left untouched as controls; (3) three with natural kelp forest were cleared of kelp, and (4) three with natural kelp forest were left as controls. The results showed that kelp recruited in areas that had been cleared of kelp and encrusting organisms eventually dominated the understorey community in those areas. However, kelp recruits were not found in areas where turf algae had been removed and the understorey community was, instead, firstly occupied by filamentous algae and turf algae in later stages. These indicated

that turf algae could inhibit the recruitment of kelp for some reasons other than their physical presence in that area (Kennelly 1987).

Marine algae recolonize cleared patches of substratum either through vegetative propagation or by recruitment from propagules. Given the distinct seasonal nature of the growth of *Hypnea charoides* and the rarity of cystocarpic plants in Ping Chau (see Chapter 2), it would be interesting to find out how populations of this species reestablish themselves along the rocky shore of the island during winter and spring. There are two possible scenerios. It is possible for a perennating base or some "germling banks" of *H. charoides* to be present throughout the year and new growths for each year are simply regenerations from this base or from spores in the "germling banks". On the other hand, all new growths may represent new recruitment. Different treatments were carried out in this study to try to ascertain the strategy employed by populations of *H. charoides* in reestablishing themselves annually.

## 3.2 Materials and Methods

### 3.2.1 Study site

The study site of the present experiment was on the rocky shore in A Ma Wan. This area is a sheltered beach, which is only subjected to occasional strong waves created by typhoons. The siltstone substratum forms a series of slightly inclined terraces (15° to 20°) which are always covered with sediments and an algal mat composed mainly of tuft red algae. In winter, a number of marine algae and a population of *Hypnea charoides* also grow densely on the surface of these terraces at depths of −1 to −3 m CD (see Chapter 2). The upper parts of these terraces are sometimes exposed at the lowest tidal levels during summer.

### 3.2.2 Clearing experiment

Clearing experiment was carried out by SCUBA from November 1997 to June 1999. Two types of clearing were executed, one with all the existing vegetation and sessile invertebrates removed by a chisel (chiselled plots) and the other with the same treatment but with the top 2 to 3 mm of the rock surface further removed by a hammer (hammered plots) (Fig. 3.1). Experimental plots (25 x 25 $cm^2$) were cleared on a monthly basis (bimonthly during summer and early fall, from June to October) and were haphazardly located on the inclined terraces around a 10 x 10 $m^2$ zone at depths of –1 to –2 m CD. The two types of experimental plots were set up in pairs next to each other and three pairs (four in November 1997) were created within a zone of 2 x 2 $m^2$ during each clearing. Several untreated areas (25 x 25 $cm^2$, n = 3 to 8) were also haphazardly chosen near the clearing plots (less than 3 m away from the plots) during each observation (except in January 1998 and March 1999). These served as the control plots. Observation was made approximately one month after clearing and on a monthly basis thereafter (bimonthly during summer and early fall). A quadrat with 25 small squares (5 x 5 $cm^2$ each) was placed on each experimental plot and picture of each small square was recorded with an underwater video camera. All the clearing and control plots were observed *in situ* during each visit and further investigation on them was carried out in the laboratory based on the video tapes recorded.

### 3.2.3 Investigation on the clearing and control plots

Species composition, percentage cover, species richness and Brillouin's species diversity index for all the clearing and control plots were investigated.

#### 3.2.3.1 Species composition

Identification of species recruited into the clearing and control plots was carried out *in*

*situ* and in the laboratory based on the video images. Only erect species recognizable with naked eyes were identified. Samples originally present in the cleared areas were collected before clearing and/or additional samples from control plots were collected and brought back to the laboratory for examination to aid in species identification. The presence of all recognized algal species in chiselled, hammered and control plots was recorded respectively during each observation. Differences in species composition among these three types of areas and between the two growing seasons were compared.

3.2.3.2 Percentage cover

The quadrat with 25 small squares (5 x 5 $cm^2$ each) was used. The percentage cover of each identified algal species present in each experimental plot (both clearing and control) was the relative portion of the quadrat covered by the canopy of that species as shown on the video tapes (see Brower *et al.* 1997). This was first estimated from each small square (i.e. 5 x 5 $cm^2$) of the quadrat and the resultant percentage cover of a studied species in one quadrat was obtained by calculating the mean of the cover values of all 25 small squares. The final percentage cover (i.e. the mean value of the replicates) of different algal species and their changes over time in chiselled, hammered and control plots were recorded and compared.

3.2.3.3 Species richness

The number of each algal species present in clearing and control plots was counted. Several filamentous or tuft red algae, which consist mainly of *Centroceras* spp. and *Hypnea* spp., were usually entangled with one another and thus could not be distinguished individually. These algae were collectively grouped under a single category named "the algal complex". It was treated as similar to a single species in all

calculations for species richness and for all statistical analyses.

3.2.3.4 Species diversity

The frequency of appearance of a given species within the clearing and control plots was used in the calculation for species diversity index. The quadrat with 25 small squares (5 x 5 $cm^2$ each) was placed over the experimental plot and the number of small squares in which a specific algal species appeared was counted. This was then divided by the total number of small squares of the quadrat (i.e. 25) to obtain a percentage frequency. Since these data were obtained non-randomly from a quadrat, the information-theoretic diversity measure of Brillouin (1962) was suggested (Zar 1984, Brower *et al.* 1997). The calculation is as follows:

$$H = (\log N! - \Sigma[\log n_i!])/N$$

where H = Brillouin's index (of a single experimental plot)

$n_i$ = number of individuals (i.e. frequency of a given species in that experimental plot)

N = total number of individuals (i.e. summation of the frequencies of all the algal species in that clearing area)

3.2.4 Statistical analyses

All statistical analyses were carried out with SigmaStat (Jandel Scientific Software). Before the analyses, data were first tested for normality by Kolmogorov-Smirnov test and homogeneity of variance by Levene Median test. Log (x + 1) transformation was used when the data could not meet the assumptions of the parametric tests. Other methods of transformation provided by the software were also attempted where

necessary. Since the parametric assumptions could not be met after all attempts of transformation, non-parametric analyses, where available, were applied instead.

Kruskal-Wallis One Way ANOVA on Ranks was used to evaluate changes in the species richness and diversity in the control plots over time. Two Way Repeated Measures ANOVA (Time vs Treatment) was used to compare differences in the species richness and diversity between the two treatments (chiselled vs hammered) observed on the same clearing plots over time. As there are no non-parametric tests equivalent to Two Way Repeated Measures ANOVA, the latter was used even though assumption of normality in the data was not always met. Differences in the species richness and diversity between chiselled and hammered plots cleared at different times but observed within the same month were further evaluated using Mann-Whitney Rank Sum Test. Since there were no significant differences between the two treatments in both tests (Two Way Repeated Measures ANOVA and Mann-Whitney Rank Sum Test), data were then pooled for the subsequent analyses. Kruskal-Wallis One Way ANOVA on Ranks was applied to test the significant differences in the species richness and diversity between clearing and control plots measured in the same month while Mann-Whitney Rank Sum Test was used to test those measured one month after clearing (i.e. the first record after clearing) among different experimental clearings with control plots. All post-hoc pairwise multiple comparisons were done using Dunn's Method for Kruskal-Wallis One Way ANOVA on Ranks and Student-Newman-Keuls Method for Two Way Repeated Measures ANOVA.

## 3.3 Results

Creation of experimental clearings started in November 1997 and the last set was made in April 1999. Monthly observation of the experimental plots started in January

1998 after the plots were first cleared in November 1997. This was continued for the next 14 months and ended in June 1999. Totally 13 sets of experimental clearings were created throughout the study period.

### 3.3.1 Species composition

Table 3.1 represented a list of algal species that had been recruited onto chiselled, hammered and control plots throughout the whole study period. Out of the 11 species identified, four were browns (*Colpomenia sinuosa*, *Padina arborescens*, *Padina australis*, and *Sargassum* sp.), three were greens (*Caulerpa peltata*, *Enteromorpha* sp. and *Ulva* sp.) and four were reds (*Acanthophora specifera*, *Hypnea charoides*, *Laurencia undulata* and *Spyridia filamentosa*). For those that could not be distinguished and identified, they were named either according to their morphology (e.g. encrusting brown, filamentous brown, coralline algae and filamentous red) or as unknown species. The coralline algae recorded mainly referred to those erect branches as the encrusting portions were always covered by other algal species. A complex of filamentous algae, mainly composed of *Centroceras* spp. (estimated to be 75 % in composition) together with short branches of *Hypnea* spp. (estimated to be 20 % in composition), formed a furry-like carpet covering the rocky terraces in A Ma Wan. Sands and sediments were easily trapped and fragments of other algae (e.g. *Corallina, Enteromorpha, Laurencia, Padina* and *Ulva*) were occasionally embedded in this complex (usually do not exceed 5 % in composition). Although some clearing plots appeared to be bare, they could be covered by microscopic algae like diatoms which were not readily visible to the naked eyes. As the investigation of the present study focused on the macroscopic scale, these "bare" experimental plots would be treated as having "no erect species". Microalgal recruitment was examined using artificial substrata and the results are presented and discussed in Chapter 4.

### 3.3.2 Percentage cover

Table 3.2 showed the mean percentage cover (%) of different algal species recorded in control plots from February 1998 to June 1999. The algal complex was the most dominant among all the species recorded, with mean cover always exceeded 50 % (> 90 % in 1999), except in April 1998, where the mean cover was recorded to be 47.7 ± 12.5 % (n = 4). The second dominant species were *Spyridia filamentosa* in February (17.1 ± 5.3 %, n = 5), coralline algae in March (20.5 ± 5.4 %, n = 5), *Colpomenia sinuosa* (16.8 ± 10.3 %) and coralline algae (19.5 ± 6.4 %, n = 4) in April, and coralline algae in May 1998 (10.2 ± 2.4 %, n = 4). In 1999, much fewer algal species were observed in the control plots. Species like *C. sinuosa*, *Sargassum* sp., *Laurencia undulata*, filamentous red and *S. filamentosa* were recorded only in 1998 but not in 1999, though some of them could be found scattered sparsely in areas nearby. For those which were present in both years, some only occurred in a very short period of time in 1999, like *Padina australis* and *Caulerpa peltata* (from February to May in 1998 but only in February and April respectively in 1999). Besides, many of them showed much lower percentage cover in 1999 than in 1998 (more obviously for coralline algae, with percentage cover ranged from 6.6 ± 2.7 % in February to 20.5 ± 5.4 % in March 1998 but less than 1 % in 1999).

Tables 3.3 to 3.13 presented the results in algal cover of chiselled and hammered plots cleared at different times. Similar to that observed in control plots, the algal complex dominated over the others and relatively more algal species were observed in 1998 than in 1999 in most of the clearing plots.

In Nov-97 clearings, 50 % of the chiselled (Table 3.3A) and hammered (Table 3.3B) plots were covered with *Enteromorpha* sp. in the first month of observation but this

percentage cover dropped to 16.3 ± 13.3 % in chiselled plots and 33.8 ± 13.5 % in hammered plots in February 1998. In March 1998, the algal complex remained as the dominant species (73.7 ± 9.2 % in chiselled plots and 73.9 ± 7.5 % in hammered plots) but in April 1998, more brown algae grew and covered the areas (34.2 ± 25.6 % of *C. sinuosa*, 13.7 ± 12.8 % of *P. australis* and 8.8 ± 6.6 % of *Sargassum* sp. in chiselled plots; 15.3 ± 10.6 % of *C. sinuosa*, 13.1 ± 8.4 % of *P. australis* and 8.2 ± 7.2 % of *Sargassum* sp. in hammered plots). At the end of the first growing season (May and June 1998), most species disappeared and the algal complex became thinner. During summer, no erect marine algae were seen. In 1999, relatively fewer species were observed in these clearings and algal complex covered more than 90 % of the areas. For Jan-98 clearings (Tables 3.4 A & B), filamentous brown (57.3 ± 11.7 % in chiselled plots and 77.8 ± 17.0 % in hammered plots) and *Enteromorpha* sp. (36.5 ± 10.0 % in chiselled plots and 18.1 ± 15.1 % in hammered plots) were the dominant species in the first month of observation in February 1998. In March 1998, the algal complex became dominant again (63.3 ± 5.6 % in chiselled plots and 77.7 ± 8.0 % in hammered plots). The percentage cover of *Ulva* sp. started to grow from 19.9 ± 1.9 % to 59.9 ± 22.4 % in chiselled plots and 4.5 ± 4.6 % to 33.0 ± 34.6 % in hammered plots from March to April 1998. Starting from May 1998 to the end of the study period, the patterns for both types of experimental plots followed those of Nov-97 clearings (see Tables 3.3 A & B). For Feb-98 clearings (Tables 3.5 A & B), the dominant species was the algal complex, with coverage being always more than 60 % from March to June in 1998. No erect species were observed in summer and the algal complex dominated over the others in 1999, similar to those observed for Nov-97 and Jan-98 clearings (see Tables 3.3 & 3.4).

In Mar-98 clearings (Tables 3.6 A & B), it was much more obvious that the algal

complex was the dominant species (over 90 % in both types of clearing plots) in both 1998 and 1999 than those observed in the clearing plots mentioned above. Although many other algal species were recruited in the first month of observation in April 1998, all of them did not exceed 1 % in percentage cover except for *Enteromorpha* sp. (2.5 ± 4.4 %) in hammered plots (Table 3.6B). No erect marine algae were found in summer. Similar patterns were observed in both Apr-98 (Tables 3.7 A & B) and May-98 (Tables 3.8 A & B) clearings, with more than 90 % of the algal complex but mostly less than 5 % of other algae in all other months of observation, except in the chiselled plots of May-98 clearings (Table 3.8A), in which there was 14.7 ± 13.7 % of *Ulva* sp. in February 1999. Other than the algal complex, there were no other algal species recruited in the hammered plots of both Apr-98 (Table 3.7B) and May-98 (Table 3.8B) clearings during the first month of observation.

Algal recruitment pattern in Aug-98 clearings also showed that the algal complex was the dominant species (exceeding 98 % in percentage cover) except in the first (November 1998) and the last (June 1999) months of observation when there were no erect algae found in both types of clearing plots (Table 3.9). In Nov-98 clearings (Table 3.10), no algal species were recruited other than the algal complex during the first month of observation in December 1998. This was true for both chiselled and hammered plots and the percentage cover of the algal complex remained over 90 % until June 1999. For Dec-98 clearings (Table 3.11), however, relatively more species were recruited in chiselled plots during the first month of observation in February 1999. The algal complex was not as dominant as that observed in Aug-98 and Nov-98 clearings. Its percentage cover was less than 90 % in February and March 1999. Relatively larger areas of Dec-98 clearings were covered by other species like *C. sinuosa* (11.2 ± 17.7 % in February and 13.1 ± 15.0 % in March for chiselled plots;

19.8 ± 34.1 % in February and 12.3 ± 21.4 % in March for hammered plots), *P. australis* (6.3 ± 2.4 % in March and 6.9 ± 6.6 % in April for chiselled plots; 4.8 ± 8.3 % in March for hammered plots) and *Ulva* sp. (5.7 ± 5.4 % in February and 5.0 ± 4.4 % in March for chiselled plots).

Comparing with the above clearing plots, much fewer species were recruited in plots cleared in 1999 (Tables 3.12 & 3.13). In Jan-99 clearings, coralline algae (0.1 ± 0.1 %) and the algal complex (1.9 ± 2.4 %) were recruited in the chiselled plots and only the algal complex (1.1 ± 1.8 %) was recruited in the hammered plots during the first month of observation in February 1999 (Table 3.12). Algal complex remained dominant in March and April (over 90 %) in 1999. Apart from the algal complex, the percentage cover of all other algae did not exceed 3 %. For the rest of the 1999 clearing plots (Feb-99, Mar-99 and Apr-99 clearings in Table 3.13), no other algae were observed except for the algal complex. The only exception was found in Mar-99 clearings, with 0.5 ± 0.6 % (chiselled plots) and 0.1 ± 0.1 % (hammered plots) of *P. australis*.

### 3.3.3 Species richness

In A Ma Wan, algal plants were found to be growing densely along the shore during winter but completely died off in summer (Fig. 3.2). Statistical analysis indicated that the number of species (species richness) was significantly different (Kruskal-Wallis One Way ANOVA on Ranks, $n = 12$, $p < 0.05$) during different times of observation (see also Appendix A Table A1 for the post-hoc test). In control plots, the number of species appeared to be highest during the growing season (February to June) in 1998, with a maximum of 8.4 ± 2.0 species in March. It dropped and remained quite low during the following summer. No recognizable algal species were recorded in August. The next growing season started in late November 1998 with 0.7 ± 0.5 number of

species and December 1998 with a single species recorded. However, the highest number of species was only 3.2 ± 0.4 in April 1999. Unlike in June 1998, when some encrusting brown algae and the algal complex were observed (see Table 3.2), all algal species disappeared in June 1999.

In general, the patterns of change in species richness for most of the clearing plots followed that of the control plots (Fig. 3.3). For plots cleared in November 1997, the mean number of species in chiselled plots was 2.0 ± 0.0 when they were first observed in January 1998 (Fig. 3.3A). This number rose to its maximum of 7.8 ± 1.0 in March 1998 and dropped gradually to its minima of 0.5 ± 0.6 in both August and November 1998. Though it increased again in the next growing season (January to June 1999), the highest number of species recruited was only 2.8 ± 0.5 in April 1999, which was much lower than that recorded in March 1998. Similar pattern was observed in hammered plots for Nov-97 clearings in which the mean number of species increased from 2.0 ± 0.0 in January 1998 to its maximum of 8.3 ± 0.5 in March 1998. The minimum value (0.3 ± 0.5) was recorded in November 1998 and this number rose to 2.5 ± 0.6 in February 1999 and 2.5 ± 1.3 in April 1999 in the second growing season. The results of Jan-98 clearings (Fig. 3.3B) were similar to those observed in Nov-97 clearings. The highest number of recruits was found in March 1998 for both chiselled (9.0 ± 0.0) and hammered (8.0 ± 1.0) plots, while the lowest number of recruits appeared to be the same in August 1998 (0.3 ± 0.6) for both chiselled and hammered plots. These values reached their maxima again in February 1999 (3.3 ± 1.2 in chiselled plots and 3.7 ± 1.2 in hammered plots) in the next growing season. Likewise, the highest number of species in both chiselled (7.7 ± 0.6 in April 1998) and hammered (7.3 ± 0.6 in April 1998) plots in Feb-98 clearings reached as high as those recorded in Nov-97 and Jan-98 clearings (Fig. 3.3C). The lowest values were found in

August 1998 (0.3 ± 0.6 for both chiselled and hammered plots) and again, these values only increased to a maximum of 2.7 ± 0.6 in April and June 1999 for chiselled plots and in April 1999 for hammered plots in the second growing season.

Experimental plots (Mar-98, Apr-98 and May-98 clearings) that were cleared near the end of the growing season showed relatively low mean number of species recruited when compared to that of Nov-97, Jan-98 and Feb-98 clearings (Figs. 3.3 D to E). In Mar-98 clearings, the mean values peaked at 3.7 ± 2.1 for chiselled plots and 4.7 ± 1.5 for hammered plots in April 1998 (Fig. 3.3D). These numbers decreased and remained quite low during summer. Maximum values in the second growing season were recorded in January (2.7 ± 0.6) and February 1999 (2.7 ± 1.2) for chiselled plots and in January 1999 (3.0 ± 1.0) for hammered plots. For Apr-98 and May-98 clearings (Figs. 3.3 E & F), no obvious peaks were observed in both 1998 and 1999. The maximum values were found in January 1999 with 3.0 ± 1.7 algal species recruited in chiselled plots and 2.0 ± 1.0 in hammered plots in Apr-98 clearings (Fig. 3.3E), and 3.0 ± 1.0 for both chiselled and hammered plots in May-98 clearings (Fig. 3.3F).

For the rest of the experimental plots that were cleared in 1998 (Aug-98, Nov-98 and Dec-98 clearings), none of them showed the number of recruits as high as that observed in other clearing plots in 1998 (Figs. 3.3 G to I). However, the number of recruits was relatively high in February and/or April 1999. In Aug-98 clearings, the highest number of recruits was recorded in February (2.3 ± 1.5) and April 1999 (2.3 ± 0.6) for chiselled plots and in April 1999 (2.3 ± 0.5) for hammered plots (Fig. 3.3G). For Nov-98 clearings, 3.3 ± 1.5 algal species recruited in chiselled plots and 3.0 ± 1.0 in hammered plots in February 1999 (Fig. 3.3 H). In comparison, 4.7 ± 1.2 species recruited in February 1999 in chiselled plots and 3.0 ± 1.7 in hammered plots cleared

in December 1998 (Fig. 3.3 I).

For experimental plots cleared in 1999 (Jan-99, Feb-99, Mar-99 and Apr-99 clearings), none of them showed great fluctuations in the change of species richness (Figs. 3.3 J to L). Relatively high number of recruits were recorded in Jan-99 clearings, in which the highest values were 2.7 ± 1.5 for chiselled plots and 2.7 ± 1.2 for hammered plots in March 1999 (Fig. 3.3J). The other clearing plots did not show values greater than these (Figs. 3.3 K & L). No recognizable algal species were recruited in June 1999 for all these four clearing plots and thus no graph was produced for Apr-99 clearings (no record in May 1998).

Species richness observed at different times was statistically significantly different (Table 3.14, Two Way Repeated Measures ANOVA, Factor = Time, $p < 0.05$) for most of the clearing plots (see also Appendix A Tables A2.1 to A2.11 for post-hoc tests), except for Feb-99 clearings in which only the algal complex was recruited in all replicates (see Table 3.13). However, species richness was not significantly different between treatments (Table 3.14, Two Way Repeated Measures ANOVA, Factor = Treatment, $p > 0.05$) in all except the Feb-98 clearings, nor was there significant interaction between time and treatment (Table 3.14). At different months of the year, different species may be found recruited into the experimental plots but the number present in either the chiselled or hammered plots remained very similar.

Differences in species richness in the two treatment plots (chiselled vs hammered) were further evaluated by comparing the species richness measured in the same month in plots with different clearing histories. As no significant difference was found in the number of species recruited between chiselled and hammered plots (Table 3.14;

further confirmed by Mann-Whitney Rank Sum Test), the data from these treatment plots were pooled. The pooled data were then compared with those of the control plots. Statistical analyses indicated that there were significant differences in the species richness between control and clearing plots (Table 3.15, Kruskal-Wallis One Way ANOVA on Ranks, $p < 0.05$, see also Appendix A, Tables A3.1 to A3.11 for post-hoc tests) at all times except for the measurement in August 1998, as there were no or very few erect species recruited in summer.

The number of species that appeared one month immediately after clearing differed significantly from time to time (Table 3.16, Mann-Whitney Rank Sum Test, $p < 0.05$, see also Appendix A Table A4 for the post-hoc test) between the clearing and control plots. This initial number was generally much lower in the clearing plots than in the control plots. There are some exceptions where the difference was not significant (e.g. May-98, Aug-98, Nov-98 and Dec-98 clearings, see Table 3.16).

### 3.3.4 Species Diversity

Mean species diversity observed in the control plots changed significantly over time (Fig. 3.4, Kruskal-Wallis One Way ANOVA on Ranks, $n = 12$, $p < 0.05$; see also Appendix A Table A5 for the post-hoc test). In general, the values were higher in the first growing season (February to June 1998) than in 1999. The diversity index rose from $0.6 \pm 0.1$ in February to $0.7 \pm 0.1$ in April 1998. It then dropped to its lowest value at $0.2 \pm 0.0$ in June 1998. Species diversity remained 0 from August to December as there was no or only one species recorded on the clearing plots (Fig. 3.2). In the second growing season (started from late December 1998), there seemed to have no great changes in mean diversity. Sharp peak(s) was/were not observed. The diversity was relatively low, with a value of only $0.2 \pm 0.1$ in January and $0.2 \pm 0.1$ in

April 1999.

Similar to the patterns observed in species richness, changes in species diversity for most of the clearing plots followed the trend observed in the control plots (Fig. 3.5 vs Fig. 3.4). In Nov-97 clearings, the mean diversity indices of chiselled and hammered plots were both found to be 0.3 ± 0.0 when the plots were first observed in January 1998 (Fig. 3.5A). Highest diversity indices for chiselled and hammered plots were respectively 0.7 ± 0.1 and 0.7 ± 0.0 in April 1998. These then dropped to 0 in August and December 1998. During the second growing season (late December 1998 to June 1999), nearly all the mean values of species diversity were lower than 0.2. Highest diversity values were recorded in June 1999 (0.2 ± 0.0 in chiselled plots and 0.3 ± 0.1 in hammered plots). In Jan-98 clearings (Fig. 3.5B), peak diversity appeared in March (0.7 ± 0.0) and April 1998 (0.7 ± 0.1) respectively for chiselled and hammered plots, whereas the lowest values were recorded in January 1999 (< 0.1 in both chiselled and hammered plots). Species diversity index was 0 in August and November 1998. In both experimental plots, the diversity values in the second growing season were highest in February 1999 (0.3 ± 0.2 in chiselled plots and 0.3 ± 0.1 in hammered plots). Similar to Nov-97 clearings, the mean values of species diversity of Jan-98 clearings recorded in June 1999 (0.3 ± 0.0 in chiselled plots and 0.2 ± 0.0 in hammered plots) were relatively high when compared to those observed in the other months in 1999. For Feb-98 clearings, the species diversity peaked in April 1998 for both chiselled (0.7 ± 0.0) and hammered (0.6 ± 0.1) plots (Fig. 3.5C). These values dropped to 0 in June and they remained as 0 until November in 1998. The mean species diversity index was mostly below 0.2 throughout the second growing season in 1999. In June 1999, however, the mean values reached 0.3 ± 0.0 for both chiselled and hammered plots, which was the highest for that growing season.

Except for the above three sets of clearing, no sharp peaks were observed in the species diversity of all the other groups of clearings (Figs. 3.5 D to K). Besides, the mean values were relatively low, generally below 0.5, when compared to those of Nov-97, Jan-98 and Feb-98 clearings. As shown in Fig. 3.5D, the mean species diversity indices in Mar-98 clearings were mostly lower than 0.2 except in January 1999, with $0.2 \pm 0.1$ in both chiselled and hammered plots, and in February 1999, with $0.2 \pm 0.2$ in chiselled plots. In Apr-98 clearings, all the values were also lower than 0.2 (Fig. 3.5E). The highest indices were recorded in the second growing season, with $0.1 \pm 0.1$ in chiselled plots and $0.2 \pm 0.1$ in hammered plots in January 1999. Similar pattern was also observed in May-98 clearings (Fig. 3.5F), where the mean values of species diversity were mostly below 0.2. The highest values were found in June 1999 ($0.3 \pm 0.0$ in chiselled plots and $0.3 \pm 0.1$ in hammered plots).

The mean species diversity of Aug-98 clearings generally did not exceed 0.1 except for hammered plots in April 1999 ($0.2 \pm 0.1$) (Fig. 3.5G). For Nov-98 clearings, the diversity values reached the highest of $0.3 \pm 0.2$ in chiselled plots and $0.2 \pm 0.1$ in hammered plots in February 1999 (Fig. 3.5H). Species diversity in both experimental plots of Dec-98 clearings were, however, slightly higher when compared to those of Aug-98 and Nov-98 clearings. This is particularly so with respect to the chiselled plots where the highest index of $0.4 \pm 0.0$ was recorded in March 1999 (Fig. 3.5I). For hammered plots, all index values did not exceed 0.2.

For those plots cleared in 1999, no great changes were observed in species diversity over time (Figs. 3.5 J to K). The highest values for chiselled and hammered plots of Jan-99 clearings were both recorded as $0.2 \pm 0.1$ in March 1999 (Fig. 3.5J). Other values were all lower than 0.2. In Mar-99 clearings, species diversity indices in

chiselled and hammered plots were both less than 0.1 in April 1999 (Fig. 3.5K). For the rest of the two clearing plots (Feb-99 and Apr-99 clearings), all the values were 0.

Species diversity at different times of observation was significantly different for most of the clearing plots (Table 3.17, Two Way Repeated Measures ANOVA, Factor = Time, $p < 0.05$, see also Appendix A Tables A6.1 to A6.9 for post-hoc tests), except for Apr-98, Feb-99 and Mar-99 clearings. However, species diversity was not significantly different between treatments (Table 3.17, Two Way Repeated Measures ANOVA, Factor = Treatment, $p > 0.05$) in all of them except for Feb-98 clearings, nor was there significant interaction between time and treatment (Table 3.17). At different months of the year, species diversity varied among different experimental plots but that recorded for either the chiselled or hammered plots remained very similar.

Similar to the analysis done on species richness, species diversity data from the two treatment plots were further evaluated among plots with different clearing histories that were measured within the same month. As no significant difference was found in species diversity indices between chiselled and hammered plots (Table 3.17; further confirmed by Mann-Whitney Rank Sum Test), the data were pooled. These pooled data were found to be statistically significantly different from those of the control plots, except for measurement in August 1998 (Table 3.18, Kruskal-Wallis One Way ANOVA on Ranks, $p < 0.05$, see also Appendix A Tables A9.1 to A9.11 for post-hoc tests).

The diversity of species among plots with different clearing histories recorded one month after clearing differed significantly (Table 3.19, Mann-Whitney Rank Sum Test, $p < 0.05$, see also Appendix A Table A8 for the post-hoc test) with that of the control

plots except for Aug-98, Nov-98 and Jan-99 clearings. This initial number in the clearing plots was generally much lower than that in the control plots. Similar to the patterns observed in species richness, control and treatment plots with different clearing histories tended to share different species diversity when the plots were first observed one or two months after clearing.

## 3.4 Discussion

Marine algae can recolonize cleared patches of substratum through different means, such as recruitment from propagules or germlings (Hruby & Norton 1979, Deysher & Norton 1982, Sousa 1984, Kennelly 1987, Stewart 1989, Ang 1991, Benedett-Cecchi & Cinelli 1993, Dye 1993), recruitment from vegetative branches (Deysher & Norton 1982) and vegetative propagation (Hansen 1977, Sousa 1979a, b, Stewart 1989, Dye 1993). However, it would be difficult to distinguish these different means of algal recruitment if only the upright parts of the algal thalli were removed during clearing experiments. It would not be easy either, to elucidate the most efficient means for the dominant species to retain their abundance in one place.

In the present study, two types of treatments (chiselled vs hammered) were applied on the experimental plots. The making of chiselled plots mimicked cleared gaps generated by natural disturbances, where some endoliths and/or basal parts of the holdfasts or prostrate axes of algae might still be found on the upper surface of the rocky substratum or in the crevices. It can hardly be certain that the chiselled plots are 100 % bare (see Ang 1985 and Airoldi 2000). The creation of hammered plots thus aimed at providing a real primary rock surface by removing the upper layer, similar to what was done by Kim (1997) and Airoldi (2000). These two types of experimental plots were cleared in pairs next to each other. It is therefore reasonable to believe that

they exerted very similar environmental conditions and received almost the same chances of recruitment. As a result, differences in patterns of recruitment observed between chiselled and hammered plots provided the opportunity to learn about whether any growth of algae was developed from the regeneration of remaining fragments or from new recruitment by dispersal agents (e.g. spores, propagules, young sporelings or some fragments/broken branches of algae). For example, if the species were present *only* on chiselled plots, they probably regenerated from the remnants on the rock surface but may not have recruited *de novo*. In contrast, if the species were present *only* on hammered plots, especially in the inner parts as there may be influences by potential marginal effects (see Kennelly 1983, Sousa 1984, Farrell 1989, Dye 1993, Kim 1997 and Airoldi 2000, but Benedetti-Cecchi & Cinelli 1993), they were likely to be recruited *de novo* from spores or other dispersal agents from elsewhere. There is also a possibility that their settlement or growth is inhibited by the presence of certain types of organisms which are originally present on the chiselled plots.

### 3.4.1 Species composition and percentage cover

The overall experimental results showed that both the disturbed (chiselled and hammered plots) and undisturbed (control plots) areas possessed more or less the same kinds of algal species. Since algal species found on hammered plots were most likely recruited from dispersing propagules, similarity in algal composition between chiselled and hammered plots suggests that algae found on chiselled plots were also recruited from dispersal agents. Regeneration from remnants on the rocky surface thus only constituted a small portion in structuring the composition of algal recruits on the experimental clearings. Further, similarity between these two types of clearing plots and control plots indicates that most marine algae in A Ma Wan were likely to be

recruited from spores or other dispersal agents rather than regenerated from the remnants left behind from the previous growing season. In southern California, parallel records of experimentally scraped and naturally exposed rock surfaces of approximately the same size that were close together showed that sequences of algal growth were similar in both situations (Stewart 1989). Likewise, the occurrence of most algal species on both the experimental clearings followed that observed in control plots (except in the first record of certain sets of clearing plots, see the following discussion), suggesting that they shared similar seasonal patterns. However, obvious differences were observed in the percentage cover of certain algal species, such as filamentous brown, *Enteromorpha* sp., coralline algae, *Spyridia filamentosa* and *Ulva* sp., between the experimental clearings and control plots.

With reference to the relative percentage cover of different algae on control plots and the experimental clearings, it was found that the algal complex was always the dominant species. This complex was mainly composed of *Centroceras* spp. and short branches of *Hypnea* spp. Its living habit is similar to that of an algal turf, which is able to cover the rocky substratum like a carpet. The roles played by an algal turf and its success in being one of the dominant colonizers in an algal community have well been documented (Hay 1981, Stewart 1983, 1989, Kennelly 1987, Kendrick 1991, Dye 1993, Whorff *et al.* 1995, Airoldi 2000). Majority of the turf formers are rhodophytes belonging to genera like *Centroceras*, *Ceramium, Gelidium*, *Hypnea*, *Laurencia*, *Polysiphonia* and groups of coralline algae (Hay 1981, Stewart 1983, 1989, Dye 1993, Whorff *et al.* 1995). Some brown and green algae also form algal turfs (Kennelly 1987, Kendrick 1991, Dye 1993). Within the samples of algal complex collected, pieces of *Enteromorpha, Ulva* and *Padina* were occasionally found, but in much smaller amounts (< 5 %, personal observation). Being a turf former is advantageous for an

alga to populate a place successfully. One of the reasons is that turf algae can spread widely on the substratum and remain dominant because of their ability to easily occupy a space by vegetative propagation. This allows them to be very successful in regaining dominance rapidly at any time of the year (Stewart 1983, 1989, Dye 1993, Airoldi 2000, see also Kendrick 1991 and Whorff *et al.* 1995). Besides, turf algae were shown to inhibit the growth of other algae, like kelps (Chapman 1984, see also Kennelly 1987). They stopped kelp settlement by occupying the space, outcompeted kelp recruits for light and harboured small invertebrates that might eat juvenile kelps (Kennelly 1987, see also Dayton *et al.* 1984 and Reed & Foster 1984). In addition, one common feature among many turf algae is that they are all associated with trapped sand and sediments (Stewart 1983, 1989, Kendrick 1991). This may be beneficial to their early colonization by possibly supplying more nutrients to the opportunistic algae or by protecting them from water movement and/or grazers (Kennelly 1983). These trapped sand and/or sediments could also be an important factor in regulating the composition of the biota (Stewart 1983). The present study site is a protected bay and thus algal bed is always covered by a layer of sediments. The algal complex, which possesses a dense intertwining network of filaments as many turfs do (Scoffin 1970), also traps sands and/or sediments (personal observation). Thus, the fact that this algal complex was able to remain dominant over the others in A Ma Wan could partly be a consequence of its ability to adapt to the presence of sediments in the habitat (Stewart 1983). Furthermore, the main constituents of the algal complex, *Centroceras* spp. and *Hypnea* spp., were efficient at colonizing newly available substrata by both spore release and vegetative expansion (Hay 1981). The present result showed that this algal complex was not limited to the periphery of the cleared areas, but occupied the inner part of the experimental plots extensively, indicating that it was likely to have been recruited from dispersal agents. Vegetative propagation (e.g. encroachment from the

periphery) appeared to play only a small part in algal recruitment on the experimental clearings (personal observation).

The second dominant species found in the control plots, after the algal complex, was the red alga *Spyridia filamentosa*, whose maximum percentage cover of 17.1 ± 5.3 % was recorded in February 1998. Its dominance was only recorded from January to April 1998 but not in any of the other years of study. During this period, plants of *S. filamentosa* were found either loosely attached on the rocky substratum or epiphytically on the branches of *Hypnea charoides*. Its high percentage cover, however, dropped rapidly from February to March and remained relatively insignificant until the end of its growth period in April 1998. Though *S. filamentosa* was also found recruited on chiselled and hammered plots from February to April in 1998 (see Nov-97, Jan-98, Feb-98 and Mar-98 clearings), the percentage cover was only around or below 5 %. This species appeared to depend on its ability to overgrow and to attach on other algal plants (see Hay 1981) to attain the fastest and the most efficient way to spread itself widely in A Ma Wan during its explosive growth period.

After February 1998, the dominance of marine algae observed in control plots shifted from *S. filamentosa* to coralline algae in March and to *C. sinuosa* and coralline algae in April in 1998. The abundance of coralline algae persisted till May 1998 but this was not so for *C. sinuosa*. Many species of brown and red algae are common late successional species (Sousa 1984). However, the dominance of *Colpomenia sinuosa* lasted only for a short period of time (mainly in April 1998) and no records of this species were found in any of the experimental plots thereafter. In contrast, coralline algae persisted for a little bit longer (up to May 1998) and their percentage cover remained relatively high (> 10 %) in control plots. Nonetheless, the percentage cover

of coralline algae was only recorded to be around or below 5 % in other clearing plots in all these different months of observation, suggesting that though coralline algae could be recruited by dispersal propagules, they depended much more on their basal crusts, which had been cleared off in chiselled and hammered plots, to retain their dominance and persistence in an area. The success of some coralline algae like *Corallina* spp. in becoming established over rock surfaces and in persisting from year to year as the dominant algal species in southern California was documented by Stewart (1989). These species share many attributes which appear to be adaptive to the specific habitat. For example, their basal crusts survive more than a year under sands. They are seldom removed from rocks unless the rock itself splits and is broken away. They disperse by spores coupled with vegetative propagation (Stewart 1989). Some crustose coralline algae persist by being able to colonize a variety of marine habitats and through persistence in highly disturbed environments (Kendrick 1991). Breitburg (1984), however, found that encrusting coralline algae competed poorly for primary space but they succeeded in being relatively resistant to grazing. The present results indicated that coralline algae in A Ma Wan could regenerate from the remnants left behind after scraping off their basal crusts (chiselled plots) and could also be recruited from dispersal propagules (hammered plots). Nevertheless, they relied much more on their basal crusts (control plots) to retain their dominance and persistence. They exhibited different strategies (e.g. dispersal by spores coupled with vegetative propagation) to allow them to be successful in colonizing and occupying the area.

In general, the percentage cover of all the algal species recorded on the clearing plots (both chiselled and hammered) was much lower than that recorded in control plots. In constrast, the percentage cover of filamentous brown algae and/or *Enteromorpha* sp. on Nov-97 and Jan-98 clearings in January and February 1998 and that of *Ulva* sp. on

Jan-98 clearings in March and April 1998 were much higher. Among the many algal taxa, some species are able to quickly colonize new space, and hence are regarded as the early colonizing/successional species or "fugitive species" (Dayton 1975, Stewart 1989). Many reports indicate that the most commonly found fugitive species are the ephemeral greens, especially *Enteromorpha* and/or *Ulva* (Hruby & Norton 1979, Sousa 1979a, b, 1984, Jernakoff 1983, 1985, Santelices & Norambuena 1987, Kim 1997, see also Fong *et al.* 1996, Dayton 1972 and Dye 1993). In the Ellwood algal community, Sousa (1979b) demonstrated that when a space was cleared, the early successional species (e.g. *Ulva*) would usually be the first to colonize and dominate because of their evolved life history characteristics, such as the production of large numbers of motile propagules (less seasonal than other algae) which grew rapidly to maturity. Moreover, once these early colonizers had become established, they would resist the invasion of subsequent algal colonizers or suppressed the growth of those already on the site (Sousa 1979b). In the present results, high percentage cover of filamentous brown and green algae, *Enteromorpha* sp. and *Ulva* sp., recorded in the first few months of observation in Nov-97 and Jan-98 clearings indicated that they were able to quickly recruit on new space by propagules, confirming their role as fugitive species. This was not observed in control plots because the rocky substratum was already covered with the algal complex starting in November 1997, reducing the provision of free space. The dominance of filamentous brown and *Enteromorpha* sp. observed in Jan-98 clearings in February 1998, when there were 10 species recorded in the control plots, suggested that these fugitive algae could have inhibited the growth of other algal species by fully occupying the newly opened space (see Kim 1997).

Other than the filamentous brown algae, *Enteromorpha* sp. and *Ulva* sp., the percentage covers of *Padina australis* and *Sargassum* sp. were also found to be higher

in Nov-97 clearings (also in Jan-98 clearings but not obvious) than in control plots, particularly in April and May 1998. One possibility that led to low abundance of these brown algae in control plots might be the presence of the algal complex. Turf algae were able to inhibit the settlement of other brown algae (Chapman 1984, Kennelly 1987, see also the previous discussion). Several experiments were carried out on *Sargassum muticum* in Santa Barbara harbour, California, and the results indicated that the main barrier to colonization of the rock by this brown alga was the presence of an algal cover (Deysher & Norton 1982). This implies that successful colonization requires not only the close proximity of a fertile plant but also the availability of cleared space. In some species like *Laminaria*, only a small number of plants successfully grew to visible size from a bank of several million microscopic stages even after complete removal of the algal turf, indicating the high mortality of these microscopic stages (Chapman 1984). Late dominance of *P. australis* and *Sargassum* sp. in A Ma Wan showed the commonality of certain brown (and also red) algae to occur in a later successional stages (Sousa 1984).

### 3.4.2 Implications on algal succession

Though the algal complex was the most dominant species in the control plots throughout the study period, obvious shifts in relative abundance were observed in 1998, from *Spyridia filamentosa* in February to coralline algae in March, from coralline algae in March to *Colpomenia sinuosa* and coralline algae in April and finally to coralline algae in May, suggesting the presence of a successional pattern in algal community in A Ma Wan. Similar successional change was also observed in Nov-97 and Jan-98 clearings (both chiselled and hammered plots) in 1998. The greens, *Enteromorpha* sp. and/or *Ulva* sp. as well as the filamentous brown algae (more obvious in Jan-98 clearings), were found to be one of the first colonizers. With the

drop in the percentage cover of the algal complex, the late dominant species appeared to be the browns, like *C. sinuosa*, *Padina australis* and also *Sargassum* sp. (in later stage). This dominance of brown algae occurred more obviously in Nov-97 than in Jan-98 clearings (slight dominance of *C. sinuosa* was also shown in Feb-98 clearings in April 1998), in which the main colonizers were the filamentous brown algae and *Enteromorpha* sp. followed by the algal complex and *Ulva* sp. Similar to what was recorded in the control plots, the algal complex was more dominant than all the other algae in Nov-97 and Jan-98 clearings and this dominance also prevailed in all the rest of the clearing plots during the whole period of this study.

Sousa (1979b) reviewed a number of past studies and concluded that seasonality of recruitment is crucial in determining the sequence in which species colonize newly cleared space. The species which is least seasonal in its recruitment would usually become established first, particularly if it is very fecund and can grow rapidly. Certain species characteristically dominate late in a successional sequence because they survive for a long time; that is, they withstand the suppression by species which dominate early in a successional sequence and then grow to maturity when the death of these early successional species free up more spaces (Sousa 1979b). A number of researches in the past also studied algal recruitment pattern in relation to successional change (Dayton 1972, 1975, Sousa 1984, Jernakoff 1985, Benedetti-Cecchi & Cinelli 1993, Kim 1997). Some of them found that clearings produced in different periods of the year would give rise to different algal successional patterns and clearly, the availability of dispersal agents at opportune times was a major factor (Dayton 1975, Benedetti-Cecchi & Cinelli 1993). In the present study, no successional patterns were shown in plots cleared at the end of the algal growing season (Mar-98, Apr-98 and May-98 clearings) when many marine algae were dying back. This implies that

recruitment patterns could be affected by the availability of reproductive propagules as well as the coming of hot summer.

All the experimental clearings created before or during summer of 1998, including Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98 and Aug-98 clearings, as well as the control plots became structurally similar after the summer die-off. There were no obvious differences in the recruitment patterns among them after this period. These experimental plots shared a similarity that the algal complex was far more dominant than all the other marine algae, with percentage cover always greater than 90 % (except in the chiselled plots of May-98 clearings in February 1999). It seems that the summer die-off levels off all the previous recruitment histories of these experimental plots. In central California, when harvested plots were allowed to grow undisturbed for one year, the plots reached similar levels in maturation to control populations of the species *Iridaea cordata* in 9 to 12 months (Hansen 1977), indicating that all the experimental areas would finally terminate at the same point of stability after a certain period of time (see also Dayton *et al.* 1984). Moreover, Sousa (1979a) found that in southern California, although the history of disturbance was important in the explanation of patterns in algal species composition, unique histories seemed not to affect which species would dominate at the end if a patch of habitat remained undisturbed for a long period of time. Eventually, *Gigartina canaliculata* dominated all patches, regardless of the past histories. Hence, the algal community in A Ma Wan appears to lose its recruitment pattern after the summer die-off and starts a new series of successional pattern in the following year. Likewise, the experimental plots were finally dominated by the algal complex. The new successional pattern, however, was very different from that observed in the previous year. The experimental plots cleared at the beginning or during the growing season in 1999, including Nov-98, Dec-98,

Jan-99, Feb-99, Mar-99 and Apr-99 clearings, all exhibited completely different patterns of occurrence and/or percentage cover of marine algae when compared with that observed in plots cleared in 1998. There were great variations in algal recruitment patterns between years, suggesting that the sequence of colonization and the composition of the colonizing flora were stochastic and unpredictable.

### 3.4.3 Implications for *Hypnea charoides*

In Ping Chau, *Hypnea charoides* can easily be found on the rocky terraces during its active growth period (from November/December to April/May, see Chapter 2). However, in this clearing experiment, it did not constitute a major part of the algal composition in all the experimental plots (including control, chiselled and hammered plots). In 1998, *H. charoides* was mainly observed in April while in 1999, the range of its occurrence was a bit longer, lasting from December 1998 to April 1999. One of the potential factors that affected the percentage cover of *H. charoides* in 1998 might be the overgrowth by *Spyridia filamentosa*. Besides, the real abundance of *H. charoides* in A Ma Wan could be underestimated because of the possible mixing of its thalli with the algal complex. Thus, *H. charoides* could maintain its abundance in A Ma Wan by existing as a turf former.

Because of its morphology, *H. charoides* is capable of drifting through the water column, snagging on live corals and overgrowing them (Miller & Hay 1996). It may cling to other algae with its branches or tendrils (e.g. living habits of *H. charoides* and *H. japonica* in Lung Lok Shui). Although in A Ma Wan, some clumps of *H. charoides* also grow on small tumbling cobbles or drift around the water column, majority of them are found loosely attached on stable rock surface. This indicates that *Hypnea* may prefer to settle on a stable substratum. Being one of the turf formers (see previous

discussion), *Hypnea* undoubtedly has its ability to efficiently utilize primary and secondary substrata (see Hay 1981). Of the nine most abundant epiphytes on flat rocky beaches in southern California, *Hypnea valentiae* is one of the three which are conspicuously repent with arched axes that creep over and among other thalli (Stewart 1983). Moreover, it is adapted for vegetative spread by forming thallus-to-thallus fusions without the development of distinct structures (Stewart 1989). Thus, vegetative fragmentation and propagation might be a common way for *H. charoides* to disperse its branches or clumps and quickly occupy space in A Ma Wan. Some members of Gigartinales, like *Gigartina canaliculata,* were found to be able to spread vegetatively across the rock surface by their rhizoids-like basal branches that attach onto the surface at the distal ends and creat an entirely new plant by sprouting branches at the point of contact (Sousa 1979b). Another member, *Iridaea cordata*, was also found to be derived primarily from perennation (Hansen 1977). The roles played by its perennating structure, a basal crust, are: (1) to initiate almost all blades in the population and (2) to act as a "space-saver" of prime substratum in its community at the time when the blades have died back (Hansen 1977). In *Solieria filiformis*, the stability of its free-floating populations was assured by regeneration and this helped to ensure the vegetative propagation of its unattached populations (Perrone & Cecere 1997).

In 1998, recruits of *H. charoides* were mainly observed in April, i.e. they appeared on the experimental clearings more than two months after the plots were cleared (except in Mar-99 clearings). However, in 1999, they were absent on the clearing plots created on or after November 1998 (i.e. those cleared before/during the second growing season, including Nov-98, Dec-98, Jan-99, Feb-99, Mar-99 and Apr-99 clearings) but were present only on those cleared in or before August 1998. There are some

implications to this observed phenomenon. Recruitment by spores or reproductive propagules occurred from December 1997 to April 1998, when the populations of *H. charoides* grew densely in A Ma Wan, and that from March to April 1998 obviously coincided with the period of increasing abundance of tetrasporophytes, suggesting that the *H. charoides* recruits could come from carpospores or even tetraspores (see Chapter 2).. Spore recruitment could carry on after April 1998 or the spores released at the end of the growing season might exist as some microscopic floating forms during summer and recruit when environments allowed. During the second growing season in 1999, it was possible that recruits of *H. charoides* were from regeneration of the remnants of preceding year or recruitment of vegetative branches from the population nearby. Even if recruited, *H. charoides* might first appear as algal turfs (i.e. part of the algal complex) and develop its erect plant parts only when conditions become favourable. Therefore, recruitment by spores or reproductive propagules of *H. charoides* populations may happen within a very wide window throughout the year. This supports the idea that *H. charoides* might exhibit heterotrichy in which its prostrate form (i.e. short branches embedded in the algal complex) can spread widely in open space and develop the upright thalli thereafter to build up its population (see Chapter 2).

In A Ma Wan, the algal complex was able to occupy most of the areas quickly and to spread over the rocky substratum vegetatively. When conditions were favourable, these prostrate forms would develop into an erect plant. Since these erect individuals were only loosely attached on the rock surface, they could be broken off and dispersed easily to more areas. Vegetative fragmentation can thus be an important mechanism of population recruitment for *H. charoides* during the growing season in A Ma Wan (see also Chapter 2).

### 3.4.4 Species richness and diversity

All of the experimental plots, including control, chiselled and hammered plots, generally showed greater number of species and higher species diversity during winter and spring (from January to May) than during summer in both 1998 and 1999. There was a die-off of algae in summer and fall, starting from June to September/October in 1998, during which the number of species and diversity index became relatively low. The algal complex was still observed in most of the experimental plots in June 1998. Nevertheless, it was reduced to a very thin layer. In August 1998, all the experimental plots were not entirely bare as they appeared. They were covered with a very thin layer composed of numerous tiny brown and green filaments. Apart from these, other algal species were also found recruited during this die-off period, represented by encrusting brown, filamentous brown, *Padina australis* and an unknown species (see Nov-97, Jan-98, Feb-98, Mar-98 and May-98 clearings). However, all these recruits constituted only a very minor part in the percentage cover. Nonetheless, this implies that recruitment process of marine algae in A Ma Wan occurs throughout the whole year (see also Chapters 4 & 5).

Temporal variations in species richness and diversity differ with different times of observation and provision of open space in a year. This is similar to many previous studies which documented temporal variation in recruitment of other algal communities (Hruby & Norton 1979, Deysher & Norton 1982, Reed *et al.* 1988, Ang 1991, Benedetti-Cecchi & Cinelli 1993, Kaehler & Williams 1997, Airoldi 2000). In some cases, such variation was found to be related to or coincided with certain reproductive events (Deysher & Norton 1982, Ang 1991, Benedetti-Cecchi & Cinelli 1993, Kaehler & Williams 1996). The time when a substratum was disturbed also altered the degree of variation in species richness and diversity and thus algal

recruitment pattern could be affected by the relative probability of disturbance of the area where the propagules settled (Dayton 1975, Sousa 1979a, b, see also Blanchette 1996). As suggested by Abugov (1982), temporal pattern of disturbance plays an important role in determining species abundances and diversity. Thus, in the present case, greater number of species and higher species diversity in the experimental plots were recorded in cold season, at a time when many algae grow and reproduce. This increases the availability of algal propagules, hence the chance of recruitment (Dayton 1975, Hruby & Norton 1979, Deysher & Norton 1982, Sousa 1984, Schiel 1985, Reed *et al.* 1988, Dayton *et al.* 1992, Benedetti-Cecchi & Cinelli 1993). However, a very noteworthy point is that the values recorded for both species richness and diversity were much higher in 1998 than those recorded in 1999, indicating that the patterns of algal recruitment in A Ma Wan exhibited an annual variation (see previous discussion). The real reason for this variation was not known. Such variation could be related to changes in some physio-chemincal parameters. For example, it was recorded that the concentrations of different nutrients in seawater fluctuated a lot in 1999 while they all remained very steady in 1998 (see Chapter 2). This may have influenced the subsequent growth of various marine algae. On the other hand, some unusual events, like the prolonged stay of Typhoon Babs in Hong Kong from 15-Oct to 27-Oct 1998, right before the growing season of algae, could have altered the conditions of marine habitats. Increasing water movement could have resulted in prolonged sinking and attachment of algal spores (Santelices 1990). Since turf formers can employ different strategies to occupy space, the algal complex might be able to overcome the problem of increased water motion and thus, became more dominant than all the other algal species in that particular growing season.

Although the two types of experimental plots (chiselled and hammered) and the

control plots appeared to be nearly the same in species richness and diversity most of the times, some significant differences between them were observed. This is specially so with respect to the first records in species richness and diversity of many clearing plots after clearing, indicating that whenever there was an open space, the immediate pattern of recruitment could be very different between the undisturbed areas nearby and the newly opened space. What was recruited in the opened space were early successional species (e.g. *Enteromorpha* sp., *Ulva* sp., or other filamentous algae), which were more competitive than the others, leading to a dominance of pioneering algae. Thus, species richness and diversity in clearing plots immediately after clearing would be lower than those observed in the control plots. Nonetheless, these values became more similar in later months, indicating that the ephemeral species were gradually being replaced by later successional species. The overall similarity in both species richness and diversity throughout the whole study period between experimental and control plots further supported the idea that most marine algae in A Ma Wan were recruited *de novo* and that regeneration from remnants did not contribute significantly to the overall structure of the algal recruitment patterns.

Table 3.1. A list of algal species (with abbreviations) recorded on chiselled, hammered and control plots during the study.

| | Abbreviations | Algal species |
|---|---|---|
| **Brown** | **Col** | *Colpomenia sinuosa* |
| | **EnB** | Encrusting brown |
| | **FB** | Filamentous brown |
| | **PAr** | *Padina arborescens* |
| | **PAu** | *Padina australis* |
| | **Sar** | *Sargassum* sp. |
| **Green** | **Cau** | *Caulerpa peltata* |
| | **En** | *Enteromorpha* sp. |
| | **Ul** | *Ulva* sp. |
| **Red** | **Aca** | *Acanthophora specifera* |
| | **CA** | Coralline algae |
| | **FR** | Filamentous red |
| | **Hyp** | *Hypnea charoides* |
| | **Lau** | *Laurencia undulata* |
| | **Spy** | *Spyridia filamentosa* |
| **Others** | **C** | Complex |
| | **Un1** | Unknown species 1 |
| | **Un2** | Unknown species 2 |

Table 3.2. Mean percentage cover (% ± SD) of different algal species present in control plots (n = 3 to 8) during different months of observation from February 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Feb | Mar | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Apr | Jun |
| **Brown** | | | | | | | | | | | | |
| Col | 0.1 ± 0.2 | 5.2 ± 3.7 | 16.8 ± 10.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0.1 ± 0.2 | 3.4 ± 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 1.9 ± 0.9 | 0.2 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.8 ± 0.8 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 2.0 ± 1.7 | 1.7 ± 1.5 | 3.1 ± 4.1 | 2.4 ± 3.9 | 0 | 0 | 0.2 ± 0.2 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 |
| Sar | 0 | 0.5 ± 0.5 | 0.2 ± 0.2 | 0.3 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | | | |
| Cau | 0.3 ± 0.4 | 4.6 ± 4.7 | 1.3 ± 2.4 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 2.0 ± 5.0 | 0 |
| En | 0.8 ± 0.8 | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 1.8 ± 1.7 | 0 | 0 | 0 |
| Ul | 0.2 ± 0.4 | 0.4 ± 0.6 | 3.3 ± 4.4 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0.7 ± 1.3 | 0.2 ± 0.3 | 0 |
| **Red** | | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 |
| CA | 6.6 ± 2.7 | 20.5 ± 5.4 | 19.5 ± 6.4 | 10.2 ± 2.4 | 0 | 0 | 0 | 0 | 0.2 ± 0.3 | 0.4 ± 0.5 | 0 | 0 |
| FR | < 0.1 | 1.0 ± 1.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 6.8 ± 10.3 | 0 | 0 | 0 | 0 | 0 | 1.0 ± 1.8 | 1.1 ± 1.3 | 5.4 ± 5.2 | 0 |
| Lau | 0 | 0 | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 17.1 ± 5.3 | 5.9 ± 4.2 | 1.5 ± 0.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | | |
| C | 71.0 ± 5.7 | 59.9 ± 6.9 | 47.7 ± 12.5 | 87.0 ± 5.2 | 96.6 ± 0.9 | 0 | 0 | 100 ± 0.0 | 97.0 ± 1.8 | 97.8 ± 2.2 | 91.5 ± 5.2 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 0 | 100 ± 0.0 | 99.8 ± 0.2 | 0 | 0 | 0 | 0 | 100 ± 0.0 |

Table 3.3A. Mean percentage cover (% ± SD) of different algal species present in chiselled plots of Nov-97 clearings (n = 4) during different months of observation from January 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Jan | Feb | Mar | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | | | | |
| Col | 0 | 0.4 ± 0.4 | 4.7 ± 1.8 | 34.2 ± 25.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0.2 ± 0.3 | 0.6 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 12.1 ± 6.3 | 0.1 ± 0.2 | 0 | 0 | 0 | 0.2 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 2.2 ± 2.6 | 8.1 ± 8.4 | 13.7 ± 12.8 | 10.8 ± 11.1 | 0 | 0 | 0.3 ± 0.4 | 0 | 0 | 0 | 0 | 0.3 ± 0.1 | 3.6 ± 1.2 |
| Sar | 0 | 0.1 ± 0.1 | 2.9 ± 1.1 | 8.8 ± 6.6 | 11.7 ± 4.7 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0.1 ± 0.1 | 0.2 ± 0.4 |
| **Green** | | | | | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6.5 ± 11.4 | 0 |
| En | 50.0 ± 0.0 | 16.3 ± 13.3 | 0.9 ± 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0.5 ± 0.3 | 3.3 ± 0.9 | 7.0 ± 3.9 | 0.5 ± 0.4 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 1.1 ± 2.1 | 2.4 ± 4.2 | 0 | 0 |
| **Red** | | | | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 1.3 ± 1.2 | 4.6 ± 3.3 | 4.6 ± 2.3 | 4.1 ± 2.0 | 0 | 0 | 0 | 0 | 0.4 ± 0.6 | 0.6 ± 0.4 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 4.1 ± 5.9 | 0 | 0 | 0 | 0 | 0 | 1.4 ± 2.8 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 2.4 ± 3.9 | 1.9 ± 0.5 | 1.8 ± 1.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | | | | |
| C | 50.0 ± 0.0 | 65.1 ± 15.1 | 73.7 ± 9.2 | 25.9 ± 18.5 | 72.8 ± 14.1 | 99.5 ± 0.1 | 0 | 0 | 100.0 ± 0.0 | 98.1 ± 3.4 | 98.4 ± 1.7 | 97.7 ± 4.2 | 93.3 ± 11.3 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 0 | 0 | 99.8 ± 0.2 | 99.8 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 96.2 ± 1.2 |

Table 3.3B. Mean percentage cover (% ± SD) of different algal species present in hammered plots of Nov-97 clearings (n = 4) during different months of observation from January 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Jan | Feb | Mar | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | | | | |
| Col | 0 | 1.0 ± 1.7 | 2.5 ± 2.9 | 15.3 ± 10.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0.7 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 15.8 ± 2.7 | 0.2 ± 0.2 | 0 | 0 | 0 | 0.6 ± 0.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0.7 ± 0.5 | 3.2 ± 2.0 | 13.1 ± 8.4 | 9.5 ± 7.5 | 0 | 0 | 0.4 ± 0.8 | 0 | 0 | 0 | 0 | 0.2 ± 0.2 | 5.9 ± 3.7 |
| Sar | 0 | 0 | 5.1 ± 6.1 | 8.2 ± 7.2 | 14.2 ± 11.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0.3 ± 0.5 |
| **Green** | | | | | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.2 ± 5.9 | 0 |
| En | 50.0 ± 0.0 | 33.8 ± 13.5 | 6.5 ± 9.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0.3 ± 0.5 | 1.5 ± 1.9 | 3.1 ± 3.0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0.4 ± 0.7 | 0.9 ± 0.7 | 5.1 ± 4.0 | 0.8 ± 1.6 | 0 |
| **Red** | | | | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0.7 ± 1.1 | 5.1 ± 4.5 | 3.6 ± 1.7 | 2.0 ± 0.9 | 0 | 0 | 0 | 0 | 0.2 ± 0.3 | 0.2 ± 0.2 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 1.9 ± 1.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 1.0 ± 1.5 | 2.1 ± 2.1 | 0.6 ± 0.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | | | | |
| C | 50.0 ± 0.0 | 46.7 ± 15.0 | 73.9 ± 7.5 | 54.3 ± 8.2 | 74.4 ± 13.4 | 99.3 ± 0.4 | 0 | 0 | 100.0 ± 0.0 | 99.5 ± 0.8 | 99.0 ± 0.7 | 95.0 ± 4.0 | 95.8 ± 5.9 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 0 | 0 | 99.4 ± 0.7 | 99.6 ± 0.8 | 0 | 0 | 0 | 0 | 0 | 93.9 ± 3.6 |

Table 3.4A. Mean percentage cover (% ± SD) of different algal species present in chiselled plots of Jan-98 clearings (n = 3) during different months of observation from February 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Feb | Mar | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | | | |
| Col | 0 | 0.8 ± 0.4 | 3.7 ± 4.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 57.3 ± 11.7 | 0.7 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.1 ± 2.0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0.4 ± 0.7 | 1.7 ± 1.8 | 0.6 ± 0.5 | 0 | 0 | 0.3 ± 0.3 | 0 | 0 | 0 | 0 | 0.3 ± 0.5 | 4.6 ± 3.5 |
| Sar | 0 | 1.8 ± 1.3 | 0.5 ± 0.9 | 5.4 ± 2.6 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | | | | |
| Cau | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 36.5 ± 10.0 | 3.4 ± 1.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 19.9 ± 1.9 | 59.9 ± 22.4 | 0.3 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 2.0 ± 1.7 | 6.0 ± 8.4 | 0.2 ± 0.4 | 0.5 ± 0.5 |
| **Red** | | | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 5.6 ± 1.4 | 3.3 ± 0.3 | 2.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 1.5 ± 2.0 | 0 | 0 | 0 |
| FR | 0 | 0.4 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 8.2 ± 7.6 | 0 | 0 | 0 | 0 | 3.7 ± 6.2 | 0 | 0.2 ± 0.2 | 0 | 0.9 ± 1.6 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 3.6 ± 2.9 | 1.2 ± 1.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | | | |
| C | 6.3 ± 1.7 | 63.3 ± 5.6 | 21.3 ± 13.2 | 91.5 ± 2.1 | 100.0 ± 0.0 | 0 | 0 | 96.3 ± 6.5 | 99.9 ± 0.1 | 96.3 ± 3.0 | 94.0 ± 8.4 | 97.5 ± 3.9 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0.9 ± 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 0 | 99.1 ± 1.5 | 99.7 ± 0.3 | 0 | 0 | 0 | 0 | 0 | 94.9 ± 3.0 |

Table 3.4B. Mean percentage cover (% ± SD) of different algal species present in hammered plots of Jan-98 clearings (n = 3) during different months of observation from February 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | 1999 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Feb | Mar | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | | | |
| Col | 0 | 0.7 ± 1.0 | 9.1 ± 4.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 77.8 ± 17.0 | 4.6 ± 3.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 ± 0.5 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0.4 ± 0.4 | 1.7 ± 1.7 | 0.1 ± 0.1 | 0 | 0.3 ± 0.5 | 0.4 ± 0.2 | 0 | 0 | 0.1 ± 0.1 | 0 | 1.1 ± 1.6 | 5.5 ± 2.3 |
| Sar | 0 | 0.3 ± 0.3 | 1.8 ± 0.7 | 4.0 ± 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 1.7 ± 2.9 | 0 |
| En | 18.1 ± 15.1 | 6.4 ± 1.4 | 0.4 ± 0.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 4.5 ± 4.6 | 33.0 ± 34.6 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0.3 ± 0.5 | 3.5 ± 4.5 | 7.1 ± 6.5 | 0 | 0 |
| **Red** | | | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 1.5 ± 1.1 | 4.4 ± 1.9 | 1.1 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0.7 ± 0.6 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 5.5 ± 5.1 | 0 | 0 | 0 | 0 | 2.9 ± 5.1 | 0 | 0.3 ± 0.3 | 0 | 1.5 ± 2.5 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 3.8 ± 2.5 | 2.7 ± 2.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | | | |
| C | 4.1 ± 4.7 | 77.7 ± 8.0 | 41.5 ± 21.3 | 94.7 ± 0.8 | 100.0 ± 0.0 | 0 | 0 | 96.8 ± 4.9 | 99.7 ± 0.5 | 95.5 ± 5.1 | 92.8 ± 6.4 | 95.7 ± 3.8 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 0 | 99.73 ± 0.5 | 99.6 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 94.5 ± 2.3 |

Table 3.5A. Mean percentage cover (% ± SD) of different algal species present in chiselled plots of Feb-98 clearings (n = 3) during different months of observation from March 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Mar | Apr | May | Jun | Aug | Nov | Dec | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | |
| Col | 0.1 ± 0.2 | 10.1 ± 4.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0.3 ± 0.6 | 2.5 ± 3.7 | 1.3 ± 1.7 | 0 | 0 | 3.4 ± 4.9 | 0.2 ± 0.4 | 0.1 ± 0.1 | 0 | 0.6 ± 1.0 | 9.7 ± 8.3 |
| Sar | 0.1 ± 0.2 | 0.1 ± 0.1 | 0.3 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 |
| **Green** | | | | | | | | | | | |
| Cau | 0.1 ± 0.2 | 0.3 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0.2 ± 0.2 | 7.3 ± 5.6 | 0.5 ± 0.4 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 1.8 ± 2.0 | 1.1 ± 1.0 | 0.3 ± 0.5 |
| **Red** | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 2.1 ± 1.7 | 7.0 ± 1.8 | 0.7 ± 0.9 | 0 | 0 | 0 | 0.3 ± 0.3 | 0 | 0 | 0 | 0 |
| FR | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 1.6 ± 1.0 | 0 | 0 | 0 | 0 | 1.2 ± 2.1 | 0.3 ± 0.4 | 0 | 1.3 ± 2.3 | 0 |
| Lau | 0 | 1.4 ± 2.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 2.7 ± 3.7 | 1.5 ± 0.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | |
| C | 94.1 ± 2.8 | 68.3 ± 11.1 | 97.1 ± 0.9 | 100.0 ± 0.0 | 0 | 0 | 98.3 ± 2.4 | 99.5 ± 0.4 | 98.2 ± 2.0 | 97.0 ± 3.0 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 99.9 ± 0.2 | 96.5 ± 4.8 | 0 | 0 | 0 | 0 | 89.9 ± 7.9 |

Table 3.5B. Mean percentage cover (% ± SD) of different algal species present in hammered plots of Feb-98 clearings (n = 3) during different months of observation from March 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Mar | Apr | May | Jun | Aug | Nov | Dec | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | |
| Col | 0 | 9.2 ± 4.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 7.8 ± 13.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 1.3 ± 0.1 | 1.2 ± 0.8 | 0 | 0.1 ± 0.2 | 2.5 ± 2.4 | 0 | 0 | 0 | 0.5 ± 0.3 | 11.7 ± 1.9 |
| Sar | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 |
| **Green** | | | | | | | | | | | |
| Cau | 0.1 ± 0.2 | 1.7 ± 2.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 1.1 ± 1.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 1.3 ± 1.4 | 0 | 0 | 0 | 0 | 0 | 0.9 ± 1.6 | 0.3 ± 0.4 | 0.1 ± 0.2 | 0 |
| **Red** | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 1.8 ± 1.5 | 2.9 ± 2.4 | 0.5 ± 0.6 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 1.2 ± 0.7 | 0 | 0 | 0 | 0 | 0.5 ± 0.6 | 0.1 ± 0.1 | 0 | 1.1 ± 1.9 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0.4 ± 0.5 | 1.2 ± 1.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | |
| C | 88.7 ± 15.6 | 81.3 ± 5.2 | 98.3 ± 1.0 | 100.0 ± 0.0 | 0 | 0 | 99.5 ± 0.8 | 99.0 ± 0.8 | 99.7 ± 0.4 | 98.3 ± 1.6 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 99.9 ± 0.1 | 97.5 ± 2.4 | 0 | 0 | 0 | 0 | 88.3 ± 1.8 |

Table 3.6A. Mean percentage cover (% ± SD) of different algal species present in chiselled plots of Mar-98 clearings (n = 3) during different months of observation from April 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | |
| Col | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0.4 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0.4 ± 0.7 | 0 | 0 | 0 | 0.9 ± 0.5 | 0.3 ± 0.6 | 0.1 ± 0.1 | 0 | 0.1 ± 0.2 | 0.3 ± 0.5 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0.8 ± 1.4 | 4.2 ± 7.3 | 0 |
| En | 0.4 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0.7 ± 0.6 | 0.4 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 0.7 ± 1.2 | 0 | 0.5 ± 0.9 | 0 |
| **Red** | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.9 ± 1.6 | 0 | 0 |
| CA | 0.1 ± 0.1 | 0.7 ± 0.6 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0.3 ± 0.5 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 9.3 ± 9.7 | 4.1 ± 3.9 | 0.7 ± 1.2 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | |
| C | 98.3 ± 1.0 | 98.5 ± 0.6 | 100.0 ± 0.0 | 0 | 0 | 99.6 ± 0.5 | 90.5 ± 9.6 | 94.9 ± 2.9 | 97.5 ± 2.6 | 95.0 ± 7.3 | 0 |
| Un1 | 0 | 0 | 0 | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 99.8 ± 0.4 | 99.1 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.6B. Mean percentage cover (% ± SD) of different algal species present in hammered plots of Mar-98 clearings (n = 3) during different months of observation from April 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Apr | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | |
| Col | 0.4 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.2 ± 2.1 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0 | 0 | 0 | 1.1 ± 1.0 | 0.1 ± 0.1 | 0.1 ± 0.2 | 0 | 0.9 ± 1.5 | 0.7 ± 1.0 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 |
| En | 2.5 ± 4.4 | 0 | 0 | 0 | 0 | 0 | 0.5 ± 0.1 | 0 | 0 | 0 | 0 |
| Ul | 0.3 ± 0.1 | 0.8 ± 1.2 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0.5 ± 0.6 | 0 | 0 |
| **Red** | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0.7 ± 0.6 | 0.3 ± 0.3 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | 0.3 ± 0.5 | 2.0 ± 1.8 | 0.1 ± 0.2 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | |
| C | 95.8 ± 4.7 | 98.8 ± 0.9 | 100.0 ± 0.0 | 0 | 0 | 99.5 ± 0.3 | 97.4 ± 1.9 | 99.7 ± 0.3 | 98.5 ± 1.4 | 98.1 ± 3.0 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 100.0 ± 0.0 | 98.9 ± 1.0 | 0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.7A. Mean percentage cover (% ± SD) of different algal species present in chiselled plots of Apr-98 clearings (n = 3) during different months of observation from May 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| EnB | 0.6 ± 1.0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0.1 ± 0.1 | 0.3 ± 0.5 | 0 | 0.2 ± 0.4 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0.3 ± 0.6 | 0.1 ± 0.1 | 0 | 5.2 ± 9.0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0.3 ± 0.6 | 0.5 ± 0.9 | 0 | 0 |
| **Red** | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0 | 0 | 0.4 ± 0.7 | 0.1 ± 0.2 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0.6 ± 1.0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | |
| C | 99.4 ± 1.0 | 99.9 ± 0.2 | 0 | 0 | 99.7 ± 0.6 | 99.3 ± 0.5 | 98.7 ± 1.3 | 94.3 ± 9.9 | 99.8 ± 0.4 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 100.0 ± 0.0 | 99.9 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.7B. Mean percentage cover (% ± SD) of different algal species present in hammered plots of Apr-98 clearings (n = 3) during different months of observation from May 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | May | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.9 ± 1.5 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0 | 0 | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | 2.5 ± 3.9 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0.2 ± 0.4 | 1.1 ± 2.0 | 0 | 2.6 ± 4.5 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0.5 ± 0.8 | 0 | 0 |
| **Red** | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0 | 0 | 3.1 ± 5.3 | 0.5 ± 0.5 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | |
| C | 100.0 ± 0.0 | 100.0 ± 0.0 | 0 | 0 | 99.8 ± 0.4 | 95.7 ± 4.6 | 99.5 ± 0.5 | 96.9 ± 0.5 | 96.7 ± 3.4 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 100.0 ± 0.0 | 99.8 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.8A. Mean percentage cover (% ± SD) of different algal species present in chiselled plots of May-98 clearings (n = 3) during different months of observation from June 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0 | 3.1 ± 3.2 | 0.1 ± 0.2 | 0 | 0 | 0 | 0.5 ± 0.6 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 1.1 ± 0.4 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0 | 0.5 ± 0.9 | 14.7 ± 13.7 | 1.8 ± 2.0 | 0.5 ± 0.8 | 0 |
| **Red** | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0 | 0 | 0 | 0.2 ± 0.2 | 0 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0.5 ± 0.5 | 0 | 0.1 ± 0.1 | 0 | 2.4 ± 2.2 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | |
| C | 99.9 ± 0.1 | 0 | 0 | 99.3 ± 0.6 | 98.1 ± 0.9 | 85.2 ± 13.8 | 98.2 ± 2.0 | 96.6 ± 2.2 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 100.0 ± 0.0 | 96.9 ± 3.2 | 0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.8B. Mean percentage cover (% ± SD) of different algal species present in hammered plots of May-98 clearings (n = 3) during different months of observation from June 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | 1998 | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Jun | Aug | Nov | Dec | Jan | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0.1 ± 0.1 | 4.6 ± 5.9 | 0.3 ± 0.3 | 0 | 0 | 0 | 1.5 ± 0.6 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0.1 ± 0.1 | 0 | 0 |
| **Green** | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 1.1 ± 1.8 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0 | 0.7 ± 0.5 | 0.8 ± 1.2 | 3.3 ± 3.7 | 1.1 ± 1.1 | 0 |
| **Red** | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0.5 ± 0.6 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | |
| C | 100.0 ± 0.0 | 0 | 0 | 99.2 ± 0.4 | 98.1 ± 2.2 | 99.0 ± 1.4 | 96.6 ± 3.8 | 97.4 ± 0.5 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 99.9 ± 0.1 | 95.4 ± 5.9 | 0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.9. Mean percentage cover (% ± SD) of different algal species present in chiselled and hammered plots of Aug-98 clearings (n = 3) during different months of observation from November 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | Chiselled Plots | | | | | | Hammered Plots | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1998 | | 1999 | | | | 1998 | | 1999 | | | |
| Species | Nov | Dec | Feb | Mar | Apr | Jun | Nov | Dec | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0.3 ± 0.6 | 0 | 0 | 0.3 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0.4 ± 0.2 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | | | |
| Cau | 0 | 0 | 0.1 ± 0.1 | 0.3 ± 0.6 | 1.3 ± 2.3 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 1.6 ± 2.8 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 |
| **Red** | | | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0.3 ± 0.5 | 0.4 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | | | |
| C | 0 | 99.4 ± 0.5 | 99.4 ± 0.9 | 99.6 ± 0.5 | 98.3 ± 2.2 | 0 | 0 | 99.9 ± 0.1 | 99.8 ± 0.4 | 99.9 ± 0.1 | 98.0 ± 2.8 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| NES | 100.0 ± 0.0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 | 100.0 ± 0.0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.10. Mean percentage cover (% ± SD) of different algal species present in chiselled and hammered plots of Nov-98 clearings (n = 3) during different months of observation from December 1998 to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | Chiselled Plots | | | | | Hammered Plots | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1998 | 1999 | | | | 1998 | 1999 | | | |
| Species | Dec | Feb | Mar | Apr | Jun | Dec | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0.13 ± 0.23 | 0 | 0.8 ± 1.4 | 0 | 0 | 0 | 0 | 0.5 ± 0.9 | 0 |
| PAu | 0 | 1.1 ± 1.2 | 1.1 ± 1.2 | 0.9 ± 0.4 | 0 | 0 | 0.1 ± 0.1 | 0.5 ± 0.8 | 0.5 ± 0.4 | 0 |
| Sar | 0 | 0 | 0 | 0.2 ± 0.4 | 0 | 0 | 0.5 ± 0.4 | 0.1 ± 0.2 | 2.6 ± 4.5 | 0 |
| **Green** | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 3.1 ± 5.3 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 |
| **Red** | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 1.3 ± 1.0 | 0 | 0 | 0 | 0 | 0.5 ± 0.2 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | |
| C | 100.0 ± 0.0 | 94.4 ± 6.4 | 98.8 ± 1.2 | 98.1 ± 1.6 | 0 | 100.0 ± 0.0 | 99.0 ± 0.4 | 99.3 ± 1.0 | 96.4 ± 5.7 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 0 | 100.0 ± 0.0 | 0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.11. Mean percentage cover (% ± SD) of different algal species present in chiselled and hammered plots of Dec-98 clearings (n = 3) during different months of observation from February to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | Chiselled Plots | | | | Hammered Plots | | | |
|---|---|---|---|---|---|---|---|---|
| | 1999 | | | | 1999 | | | |
| Species | Feb | Mar | Apr | Jun | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | |
| Col | 11.2 ± 17.7 | 13.2 ± 15.0 | 0 | 0 | 19.8 ± 34.1 | 12.3 ± 21.4 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 1.7 ± 1.6 | 6.3 ± 2.4 | 6.9 ± 6.6 | 0 | 0.8 ± 1.2 | 4.8 ± 8.3 | 2.9 ± 2.9 | 0 |
| Sar | 0.1 ± 0.1 | 0 | 0.9 ± 0.5 | 0 | 0 | 0 | 0.6 ± 1.0 | 0 |
| **Green** | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 5.7 ± 5.4 | 5.0 ± 4.4 | 0.2 ± 0.2 | 0 | 0 | 1.3 ± 1.2 | 0.1 ± 0.1 | 0 |
| **Red** | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0.2 ± 0.2 | 0 | 0 | 0 | 0.4 ± 0.4 | 0 | 0.1 ± 0.2 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | |
| C | 81.0 ± 18.6 | 75.3 ± 11.6 | 91.9 ± 6.5 | 0 | 79.0 ± 35.7 | 81.5 ± 30.6 | 96.3 ± 4.1 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 0 | 0 | 100.0 ± 0.0 | 0 | 0 | 0 | 100.0 ± 0.0 |

Table 3.12. Mean percentage cover (% ± SD) of different algal species present in chiselled and hammered plots of Jan-99 clearings (n = 3) during different months of observation from February to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | Chiselled Plots | | | | Hammered Plots | | | |
|---|---|---|---|---|---|---|---|---|
| | 1999 | | | | 1999 | | | |
| Species | Feb | Mar | Apr | Jun | Feb | Mar | Apr | Jun |
| **Brown** | | | | | | | | |
| Col | 0 | 1.1 ± 1.4 | 0 | 0 | 0 | 2.4 ± 2.8 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 |
| Sar | 0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 |
| **Green** | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0 | 0 | 0.2 ± 0.4 | 0 | 0 |
| **Red** | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0.1 ± 0.1 | 0.1 ± 0.1 | 0 | 0 | 0 | 0.1 ± 0.1 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0.3 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | |
| C | 1.9 ± 2.4 | 98.5 ± 1.4 | 99.9 ± 0.2 | 0 | 1.1 ± 1.8 | 97.3 ± 2.6 | 99.9 ± 0.1 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 98.0 ± 2.3 | 0 | 0 | 100.0 ± 0.0 | 98.9 ± 1.8 | 0 | 0 | 100.0 ± 0.0 |

Table 3.13. Mean percentage cover (% ± SD) of different algal species present in chiselled and hammered plots of Feb-99, Mar-99 and Apr-99 clearings (n = 3) during different months of observation from April to June 1999 ('NES' = No Erect Species). Refer to Table 3.1 for the abbreviations used for different algal species.

| | Feb-99 clearings | | | | Mar-99 clearings | | | | Apr-99 clearings | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Chiselled Plots | | Hammered Plots | | Chiselled Plots | | Hammered Plots | | Chiselled Plots | Hammered Plots |
| Species | Apr | Jun | Apr | Jun | Apr | Jun | Apr | Jun | Jun | Jun |
| **Brown** | | | | | | | | | | |
| Col | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EnB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PAu | 0 | 0 | 0 | 0 | 0.5 ± 0.6 | 0 | 0.1 ± 0.1 | 0 | 0 | 0 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Green** | | | | | | | | | | |
| Cau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| En | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ul | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Red** | | | | | | | | | | |
| Aca | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| FR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hyp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Spy | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Others** | | | | | | | | | | |
| C | 100.0 ± 0.0 | 0 | 100.0 ± 0.0 | 0 | 99.5 ± 0.6 | 0 | 99.9 ± 0.1 | 0 | 0 | 0 |
| Un1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Un2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NES | 0 | 100.0 ± 0.0 | 0 | 100.0 ± 0.0 | 0 | 100.0 ± 0.0 | 0 | 100.0 ± 0.0 | 100.0 ± 0.0 | 100.0 ± 0.0 |

Table 3.14. Results of Two-Way Repeated Measure ANOVA on changes in species richness of clearing plots (Treatment: chiselled vs hammered) over time. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Month of Clearing | Source of Variance | DF | SS | MS | F | P |
|---|---|---|---|---|---|---|
| Nov-97 | Time | 13 | 579.37 | 44.570 | 65.170 | <0.0001* |
| | Treatment | 1 | 0.2230 | 0.2230 | 1.0000 | 0.3910 |
| | Time x Treatment | 13 | 6.1520 | 0.4730 | 1.6100 | 0.1238 |
| | Residual | 39 | 11.460 | 0.2940 | | |
| | Total | 66 | 597.21 | 9.0486 | | |
| Jan-98 | Time | 12 | 379.85 | 31.650 | 44.290 | <0.0001* |
| | Treatment | 1 | 0.0128 | 0.0128 | 0.0625 | 0.8259 |
| | Time x Treatment | 12 | 6.8205 | 0.5684 | 0.7084 | 0.7289 |
| | Residual | 24 | 19.260 | 0.8024 | | |
| | Total | 49 | 405.94 | 8.2846 | | |
| Feb-98 | Time | 10 | 219.61 | 21.960 | 19.000 | <0.0001* |
| | Treatment | 1 | 3.4090 | 3.4090 | 18.750 | 0.0494* |
| | Time x Treatment | 10 | 4.7580 | 0.4760 | 1.1900 | 0.3511 |
| | Residual | 20 | 7.9700 | 0.3980 | | |
| | Total | 41 | 235.75 | 5.7499 | | |
| Mar-98 | Time | 10 | 72.760 | 7.2760 | 7.6340 | <0.0001* |
| | Treatment | 1 | 0.2424 | 0.2424 | 16.000 | 0.0572 |
| | Time x Treatment | 10 | 4.0909 | 0.4091 | 0.7690 | 0.6561 |
| | Residual | 20 | 10.640 | 0.5318 | | |
| | Total | 41 | 87.733 | 2.1398 | | |
| Apr-98 | Time | 9 | 25.083 | 2.7870 | 3.5900 | 0.0101* |
| | Treatment | 1 | 0.4170 | 0.4170 | 3.5700 | 0.1994 |
| | Time x Treatment | 9 | 2.4170 | 0.2690 | 1.9900 | 0.1029 |
| | Residual | 18 | 2.4330 | 0.1350 | | |
| | Total | 37 | 30.350 | 0.8203 | | |
| May-98 | Time | 8 | 43.037 | 5.3800 | 8.7370 | 0.0001* |
| | Treatment | 1 | 0.6670 | 0.6670 | 12.000 | 0.0742 |
| | Time x Treatment | 8 | 1.3330 | 0.1670 | 0.5450 | 0.8059 |
| | Residual | 16 | 4.8890 | 0.3067 | | |
| | Total | 33 | 49.926 | 1.5129 | | |
| Aug-98 | Time | 5 | 20.220 | 4.0440 | 20.800 | <0.0001* |
| | Treatment | 1 | 0.4440 | 0.4440 | 0.8240 | 0.4557 |
| | Time x Treatment | 5 | 0.5560 | 0.1110 | 0.1400 | 0.9788 |
| | Residual | 10 | 7.9440 | 0.7940 | | |
| | Total | 21 | 29.164 | 1.3888 | | |
| Nov-98 | Time | 4 | 37.533 | 9.3830 | 16.806 | 0.0006* |
| | Treatment | 1 | 0.1330 | 0.1333 | 0.0440 | 0.8534 |
| | Time x Treatment | 4 | 0.2000 | 0.0500 | 0.0870 | 0.9840 |
| | Residual | 8 | 4.6000 | 0.5750 | | |
| | Total | 17 | 42.466 | 2.4980 | | |
| Dec-98 | Time | 3 | 54.830 | 18.278 | 28.000 | 0.0006* |
| | Treatment | 1 | 6.0000 | 6.0000 | 3.6900 | 0.1946 |
| | Time x Treatment | 3 | 3.0000 | 1.0000 | 1.6000 | 0.2853 |
| | Residual | 6 | 3.7500 | 0.6250 | | |
| | Total | 13 | 67.580 | 5.1985 | | |
| Jan-99 | Time | 3 | 21.670 | 7.2220 | 7.7610 | 0.0173* |
| | Treatment | 1 | 0.1670 | 0.1670 | 0.5710 | 0.5286 |
| | Time x Treatment | 3 | 1.5000 | 0.5000 | 1.7140 | 0.2627 |
| | Residual | 6 | 1.7500 | 0.2920 | | |
| | Total | 13 | 25.087 | 1.9298 | | |
| Mar-99 | Time | 1 | 6.7500 | 6.7500 | 27.000 | 0.0351* |
| | Treatment | 1 | 0.0833 | 0.0833 | 1.0000 | 0.4226 |
| | Time x Treatment | 1 | 0.0833 | 0.0833 | 1.0000 | 0.4226 |
| | Residual | 2 | 0.1667 | 0.0833 | | |
| | Total | 5 | 7.0833 | 1.4167 | | |

Table 3.15. Results of statistical comparison in species richness recorded within the same month between clearing (pooled data) and control plots by Kruskal-Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Months of Measurement | p (Clearing vs Control) |
|---|---|
| January 98 | (no control plots) |
| February 98 | 0.0021* |
| March 98 | 0.0089* |
| April 98 | 0.0053* |
| May 98 | 0.0004* |
| June 98 | <0.0001* |
| August 98 | 0.1402 |
| November 98 | 0.0009* |
| December 98 | 0.0011* |
| January 99 | 0.0169* |
| February 99 | 0.0102* |
| March 99 | (no control plots) |
| April 99 | <0.0001* |
| June 99 | <0.0001* |

Table 3.16. Results of statistical comparison in species richness recorded in the first month after clearing between different clearing plots (pooled data) and control plots by Mann-Whitney Rank Sum Test. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Months of Measurement | Clearing Plots | p (Clearing vs Control) |
|---|---|---|
| January 98 | Nov-97 | (no control plots) |
| February 98 | Jan-98 | 0.0043* |
| March 98 | Feb-98 | 0.0303* |
| April 98 | Mar-98 | 0.0095* |
| May 98 | Apr-98 | 0.0095* |
| June 98 | May-98 | 0.1670 |
| November 98 | Aug-98 | 0.1800 |
| December 98 | Nov-98 | (no difference)[#] |
| February 99 | Dec-98 | 0.1320 |
| February 99 | Jan-99 | 0.0043* |
| April 99 | Feb-99 | 0.0022* |
| April 99 | Mar-99 | 0.0022* |

[#]The number of species recorded in the replicates was identical.

Table 3.17. Results of Two-Way Repeated Measure ANOVA on changes in species diversity of clearing plots (Treatment: chiselled vs hammered) over time. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Month of Clearing | Source of Variance | DF | SS | MS | F | P |
|---|---|---|---|---|---|---|
| Nov-97 | Time | 13 | 6.5756 | 0.5058 | 79.820 | <0.0001* |
| | Treatment | 1 | 0.0018 | 0.0017 | 1.9600 | 0.2564 |
| | Time x Treatment | 13 | 0.0349 | 0.0027 | 1.1700 | 0.3385 |
| | Residual | 39 | 0.0897 | 0.0023 | | |
| | Total | 66 | 6.7020 | 0.1015 | | |
| Jan-98 | Time | 12 | 3.6500 | 0.3040 | 42.630 | <0.0001* |
| | Treatment | 1 | 0.0001 | 0.0001 | 0.3750 | 0.6028 |
| | Time x Treatment | 12 | 0.0549 | 0.0046 | 0.6460 | 0.7831 |
| | Residual | 24 | 0.1700 | 0.0071 | | |
| | Total | 49 | 3.8750 | 0.0791 | | |
| Feb-98 | Time | 10 | 2.0680 | 0.2068 | 21.515 | <0.0001* |
| | Treatment | 1 | 0.0189 | 0.0189 | 4.1200 | 0.1795 |
| | Time x Treatment | 10 | 0.0354 | 0.0354 | 0.7420 | 0.6784 |
| | Residual | 20 | 0.0953 | 0.0048 | | |
| | Total | 41 | 2.2176 | 0.0541 | | |
| Mar-98 | Time | 10 | 0.4474 | 0.0447 | 4.8410 | 0.0013* |
| | Treatment | 1 | <0.0001 | <0.0001 | 0.0013 | 0.9747 |
| | Time x Treatment | 10 | 0.0774 | 0.0077 | 1.9600 | 0.0961 |
| | Residual | 20 | 0.079 | 0.0039 | | |
| | Total | 41 | 0.6038 | 0.0147 | | |
| Apr-98 | Time | 9 | 0.1420 | 0.0158 | 1.6190 | 0.1835 |
| | Treatment | 1 | 0.0003 | 0.0003 | 0.1370 | 0.7467 |
| | Time x Treatment | 9 | 0.0258 | 0.0029 | 1.2780 | 0.3134 |
| | Residual | 18 | 0.0403 | 0.0022 | | |
| | Total | 37 | 0.2084 | 0.0056 | | |
| May-98 | Time | 8 | 0.3553 | 0.0444 | 6.1051 | 0.0011* |
| | Treatment | 1 | <0.0001 | <0.0001 | 0.0408 | 0.8587 |
| | Time x Treatment | 8 | 0.0228 | 0.0028 | 0.7423 | 0.6550 |
| | Residual | 16 | 0.0614 | 0.0038 | | |
| | Total | 33 | 0.4395 | 0.0133 | | |
| Aug-98 | Time | 5 | 0.0812 | 0.0162 | 4.7110 | 0.0180* |
| | Treatment | 1 | 0.0041 | 0.0041 | 0.5680 | 0.5297 |
| | Time x Treatment | 5 | 0.0078 | 0.0016 | 0.2480 | 0.9316 |
| | Residual | 10 | 0.0626 | 0.0063 | | |
| | Total | 21 | 0.1557 | 0.0074 | | |
| Nov-98 | Time | 4 | 0.2144 | 0.0536 | 5.9050 | 0.0163* |
| | Treatment | 1 | 0.0091 | 0.0091 | 0.3080 | 0.6349 |
| | Time x Treatment | 4 | 0.0130 | 0.0032 | 0.5890 | 0.6803 |
| | Residual | 8 | 0.0440 | 0.0055 | | |
| | Total | 17 | 0.2805 | 0.0165 | | |
| Dec-98 | Time | 3 | 0.3382 | 18.278 | 10.860 | 0.0078* |
| | Treatment | 1 | 0.0918 | 0.1127 | 4.8800 | 0.1578 |
| | Time x Treatment | 3 | 0.0455 | 0.0918 | 3.5800 | 0.0861 |
| | Residual | 6 | 0.0255 | 0.0152 | | |
| | Total | 13 | 0.5010 | 0.0385 | | |
| Jan-99 | Time | 3 | 0.1080 | 0.0360 | 16.487 | 0.0027* |
| | Treatment | 1 | 0.0003 | 0.0003 | 0.0995 | 0.7823 |
| | Time x Treatment | 3 | 0.0233 | 0.0031 | 1.2635 | 0.2680 |
| | Residual | 6 | 0.0368 | 0.0061 | | |
| | Total | 13 | 0.1684 | 0.0130 | | |
| Mar-99 | Time | 1 | 0.0058 | 0.0058 | 2.0066 | 0.2923 |
| | Treatment | 1 | 0.0001 | 0.0001 | 0.0896 | 0.7929 |
| | Time x Treatment | 1 | 0.0001 | 0.0001 | 0.0896 | 0.7929 |
| | Residual | 2 | 0.0029 | 0.0015 | | |
| | Total | 5 | 0.0089 | 0.0018 | | |

Table 3.18. Results of statistical comparison in species diversity recorded within the same month between clearing (pooled data) and control plots by Kruskal-Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Months of Measurement | p (Clearing vs Control) |
|---|---|
| January 98 | (no control plots) |
| February 98 | 0.0027* |
| March 98 | 0.0038* |
| April 98 | 0.0022* |
| May 98 | <0.0001* |
| June 98 | <0.0001* |
| August 98 | 0.1194 |
| November 98 | 0.0002* |
| December 98 | 0.0037* |
| January 99 | 0.0067* |
| February 99 | 0.0291* |
| March 99 | (no control plots) |
| April 99 | 0.0011* |
| June 99 | <0.0001* |

Table 3.19. Results of statistical comparison in species diversity recorded in the first month after clearing between different clearing plots (pooled data) and control plots by Mann-Whitney Rank Sum Test. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Months of Measurement | Clearing Plots | p (Clearing vs Control) |
|---|---|---|
| January 98 | Nov-97 | (no control plots) |
| February 98 | Jan-98 | 0.0043* |
| March 98 | Feb-98 | 0.0043* |
| April 98 | Mar-98 | 0.0095* |
| May 98 | Apr-98 | 0.0095* |
| June 98 | May-98 | 0.0238* |
| November 98 | Aug-98 | 0.1797 |
| December 98 | Nov-98 | (no difference)[#] |
| February 99 | Dec-98 | 0.0022* |
| February 99 | Jan-99 | 0.0649 |
| April 99 | Feb-99 | 0.0022* |
| April 99 | Mar-99 | 0.0043* |

[#]The number of species recorded in the replicates was identical.

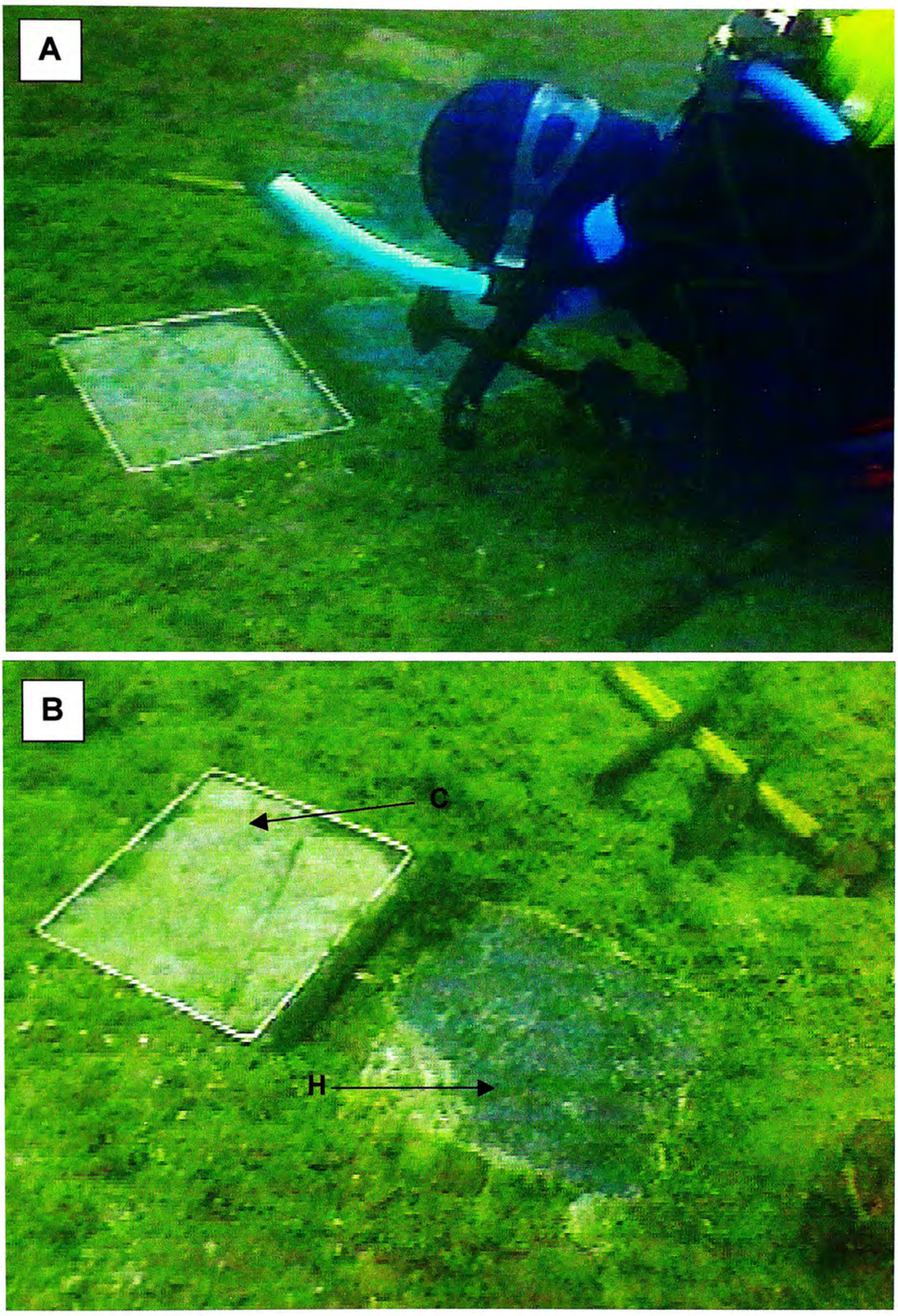


Fig. 3.1. Experimental clearing plots. (A) Experimental plots being cleared by SCUBA divers using chisels and hammers; (B) chiselled (C) and hammered (H) plots made on the rocky substratum in A Ma Wan.

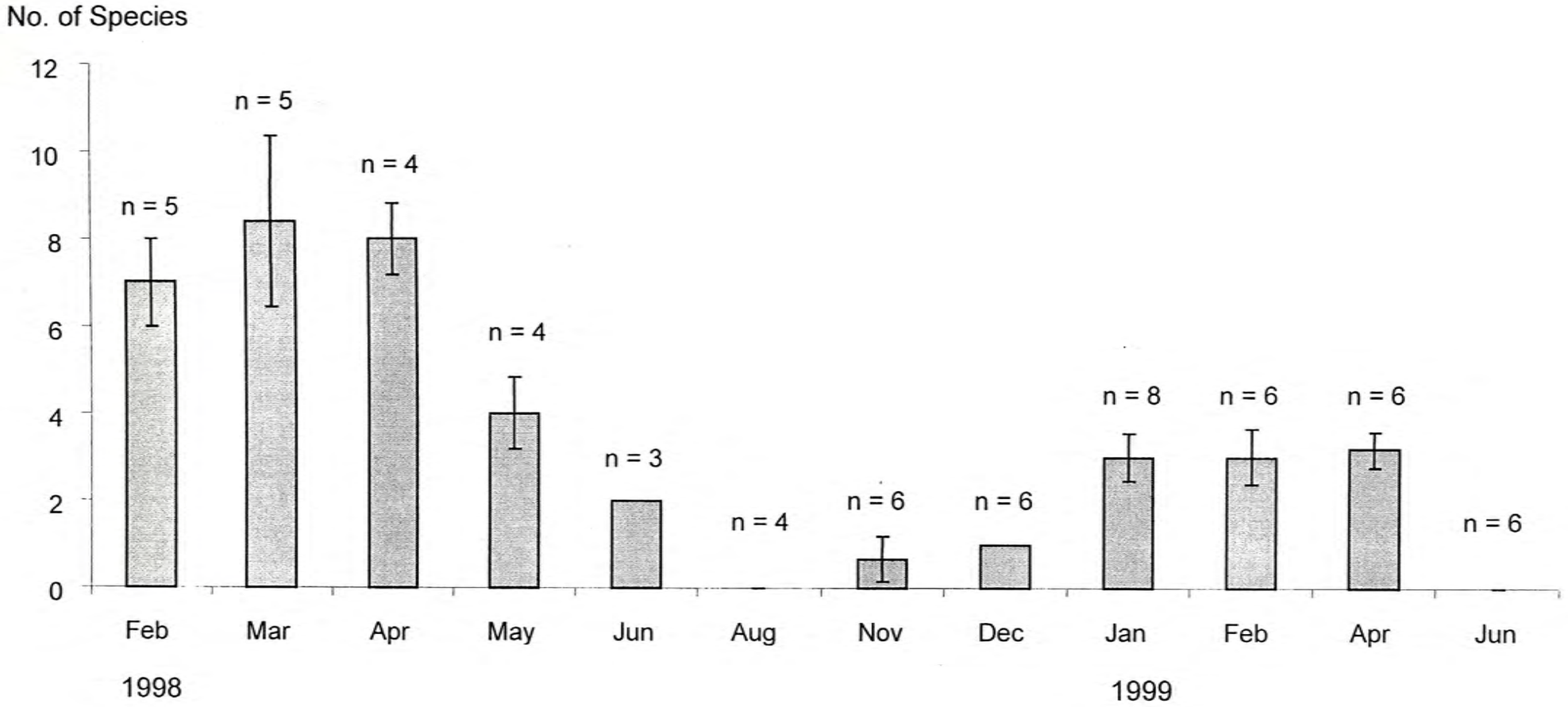


Fig. 3.2. Changes in mean species richness (± SD) in control plots (n = 3 to 8) in A Ma Wan from February 1998 to June 1999. No SD means that same number of species appeared in all the replicates.

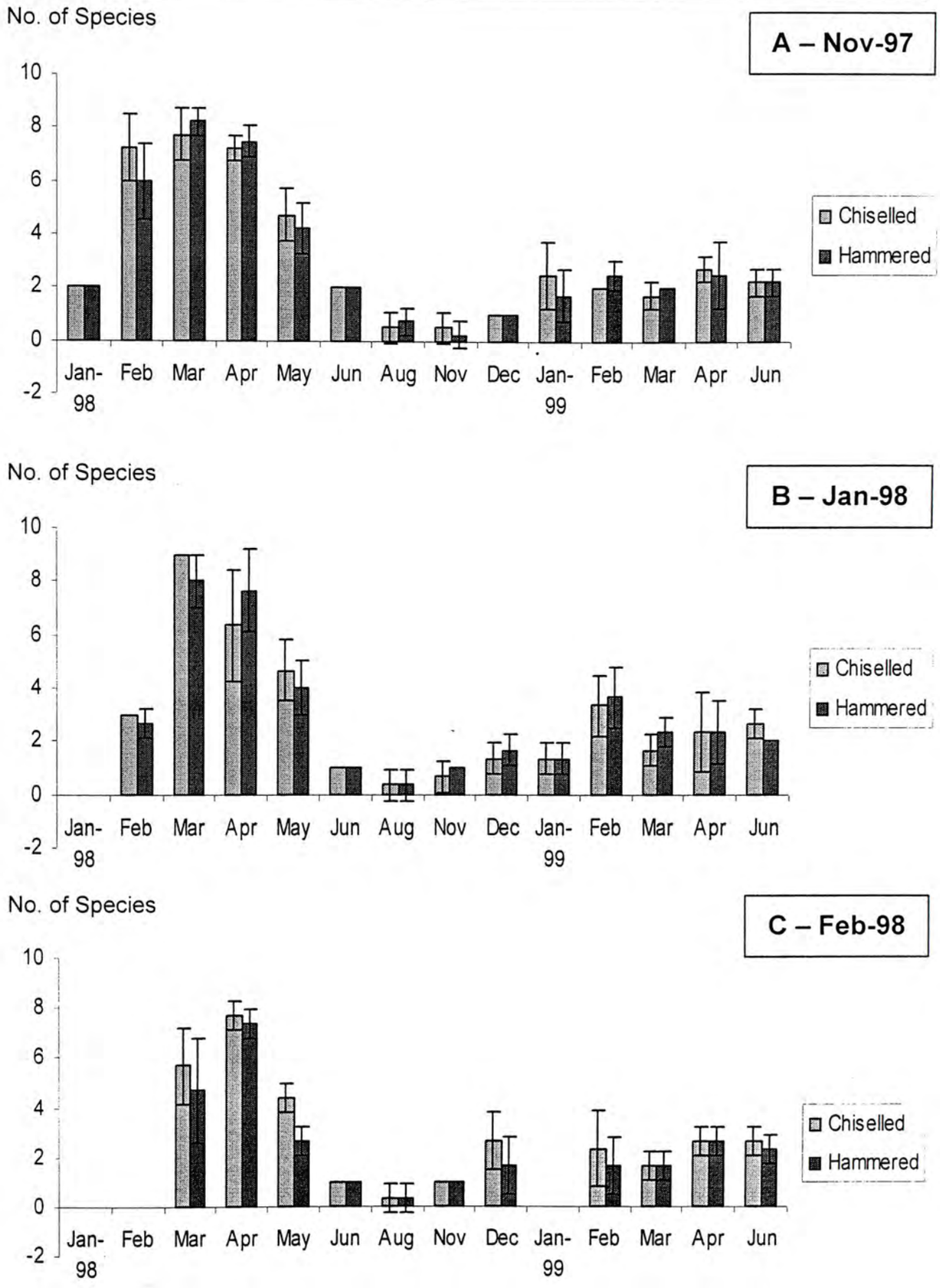


Fig. 3.3. Changes in mean species richness (± SD) during subsequent months of observations in plots cleared at different times in A Ma Wan. (A) Nov-97 clearings, n = 4; (B) Jan-98 clearings, n = 3; (C) Feb-98 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

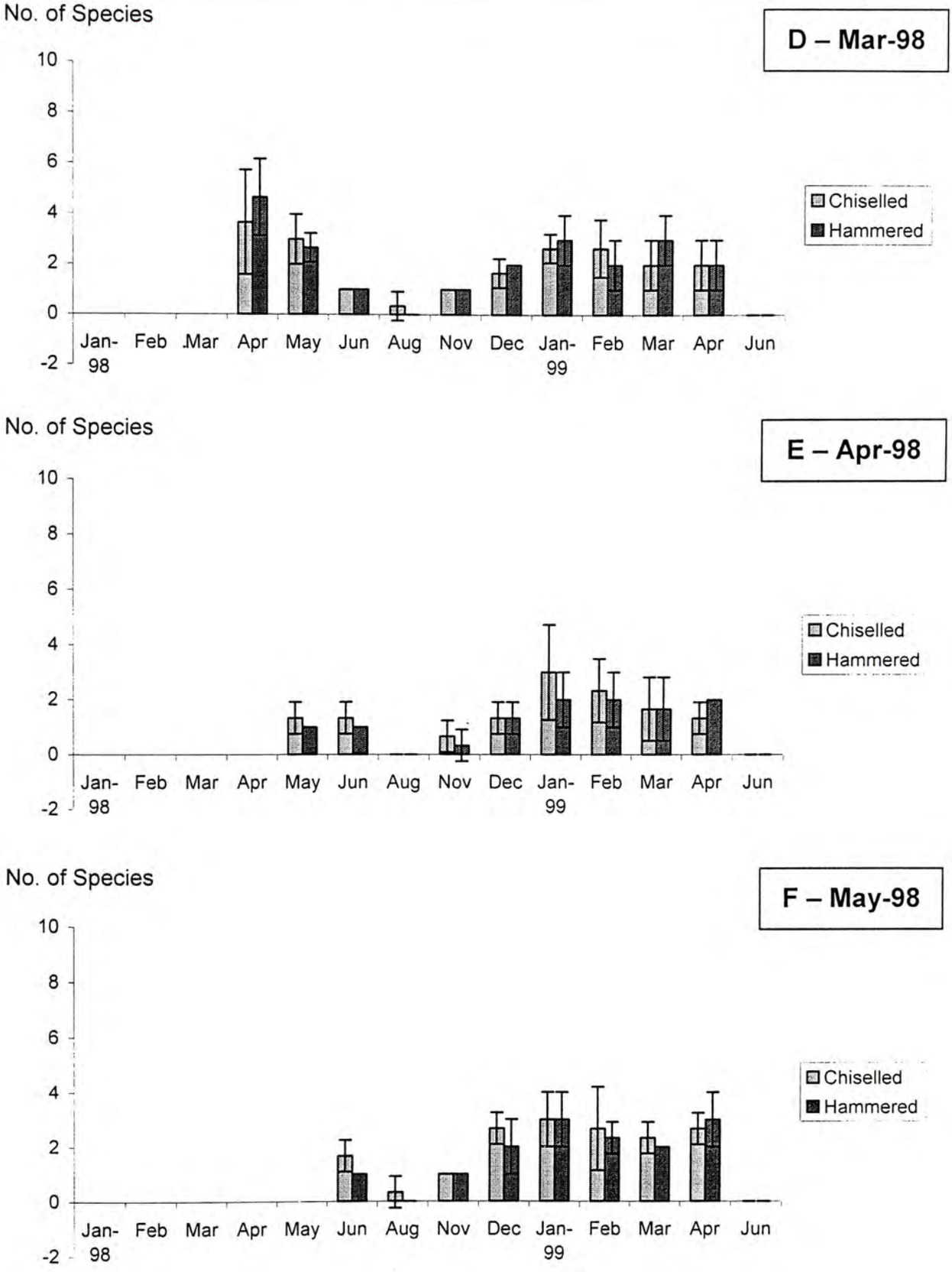


Fig. 3.3. Changes in mean species richness (± SD) during subsequent months of observations in plots cleared at different times in A Ma Wan (Cont'd). (D) Mar-98 clearings, n = 3; (E) Apr-98 clearings, n = 3; (F) May-98 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

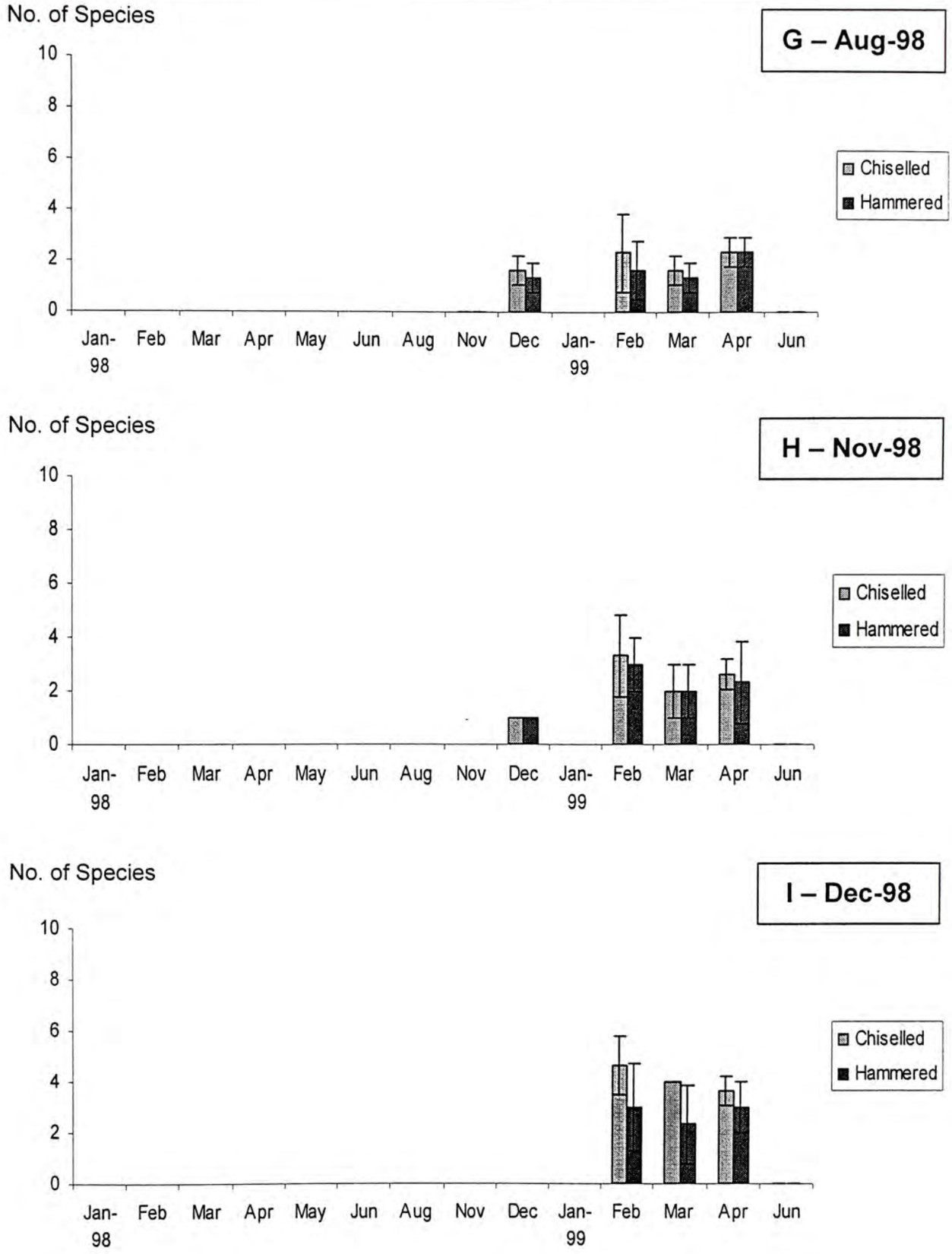


Fig. 3.3. Changes in mean species richness (± SD) during subsequent months of observations in plots cleared at different times in A Ma Wan (Cont'd). (G) Aug-98 clearings, n = 3; (H) Nov-98 clearings, n = 3; (I) Dec-98 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

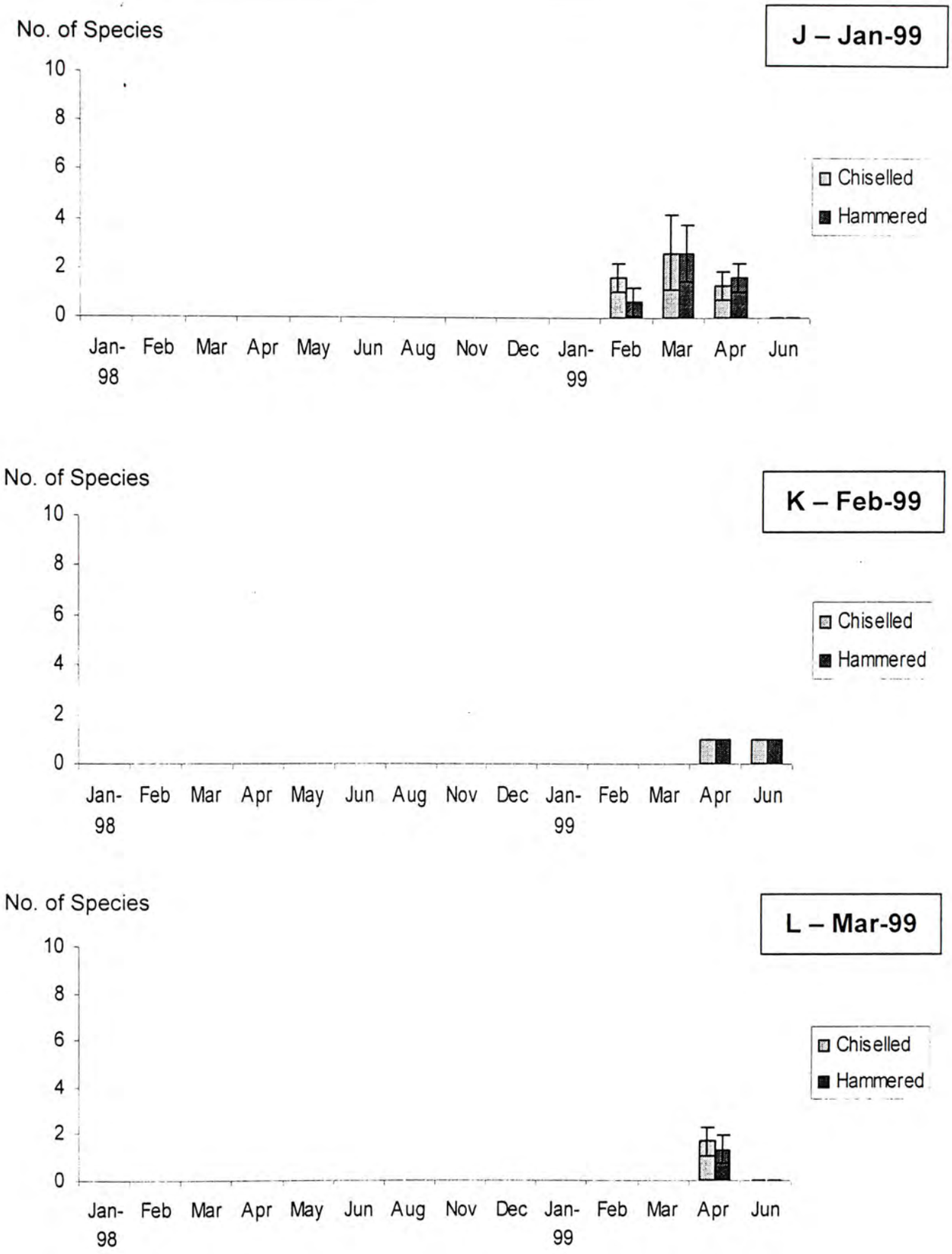


Fig. 3.3. Changes in mean species richness (± SD) during subsequent months of observations in plots cleared at different times in A Ma Wan (Cont'd). (J) Jan-99 clearings, n = 3; (K) Feb-99 clearings, n = 3; (L) Mar-99 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

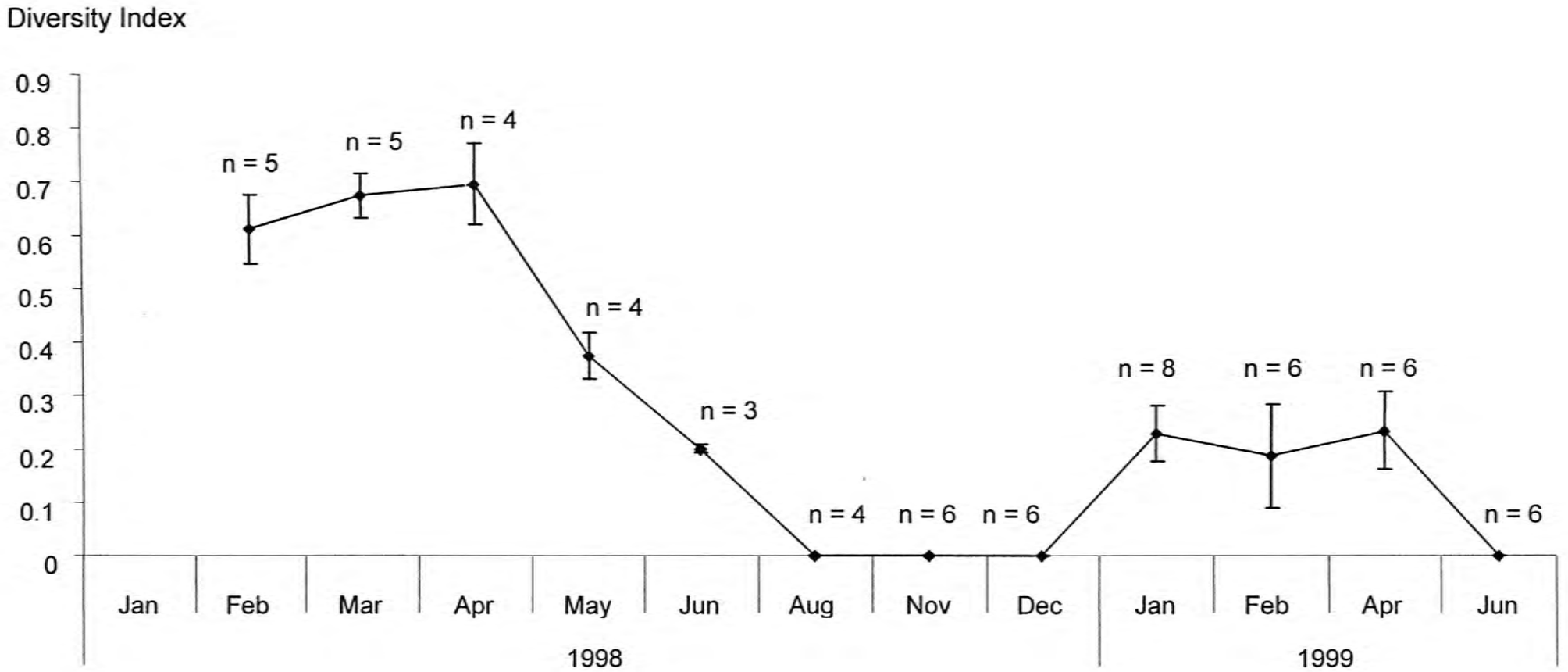


Fig. 3.4. Changes in mean Brillouin's species diversity index (± SD) in control plots (n = 3 to 8) in A Ma Wan from February 1998 to June 1999. No SD means that same number of species appeared on all the replicates.

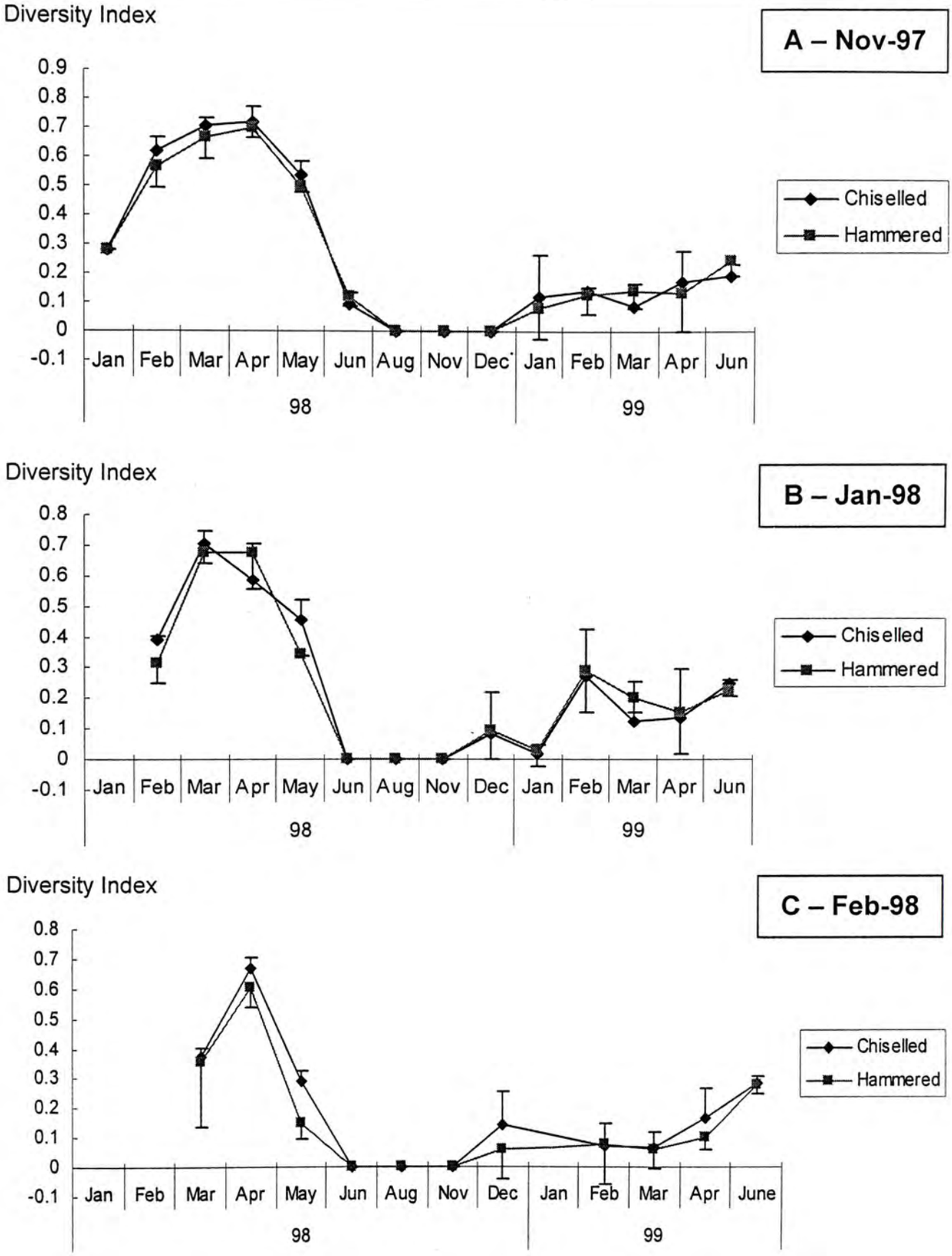


Fig. 3.5. Changes in mean species diversity (+/– SD) during subsequent months of observations in plots cleared at different times in A Ma Wan. (A) Nov-97 clearings, n = 4; (B) Jan-98 clearings, n = 3; (C) Feb-98 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

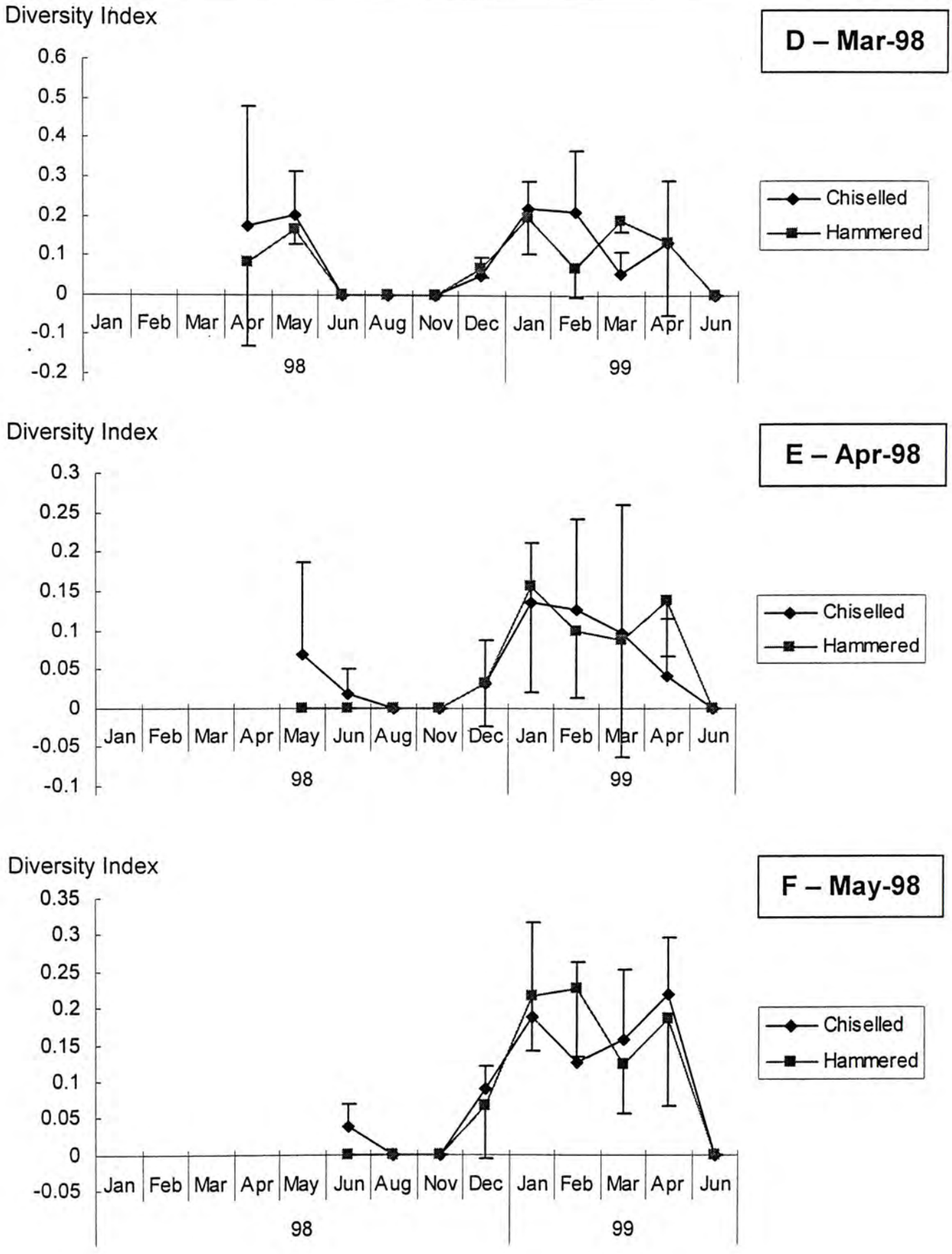


Fig. 3.5. Changes in mean species diversity (+/– SD) during subsequent months of observations in plots cleared at different times in A Ma Wan (Cont'd). (D) Mar-98 clearings, n = 3; (E) Apr-98 clearings, n = 3; (F) May-98 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

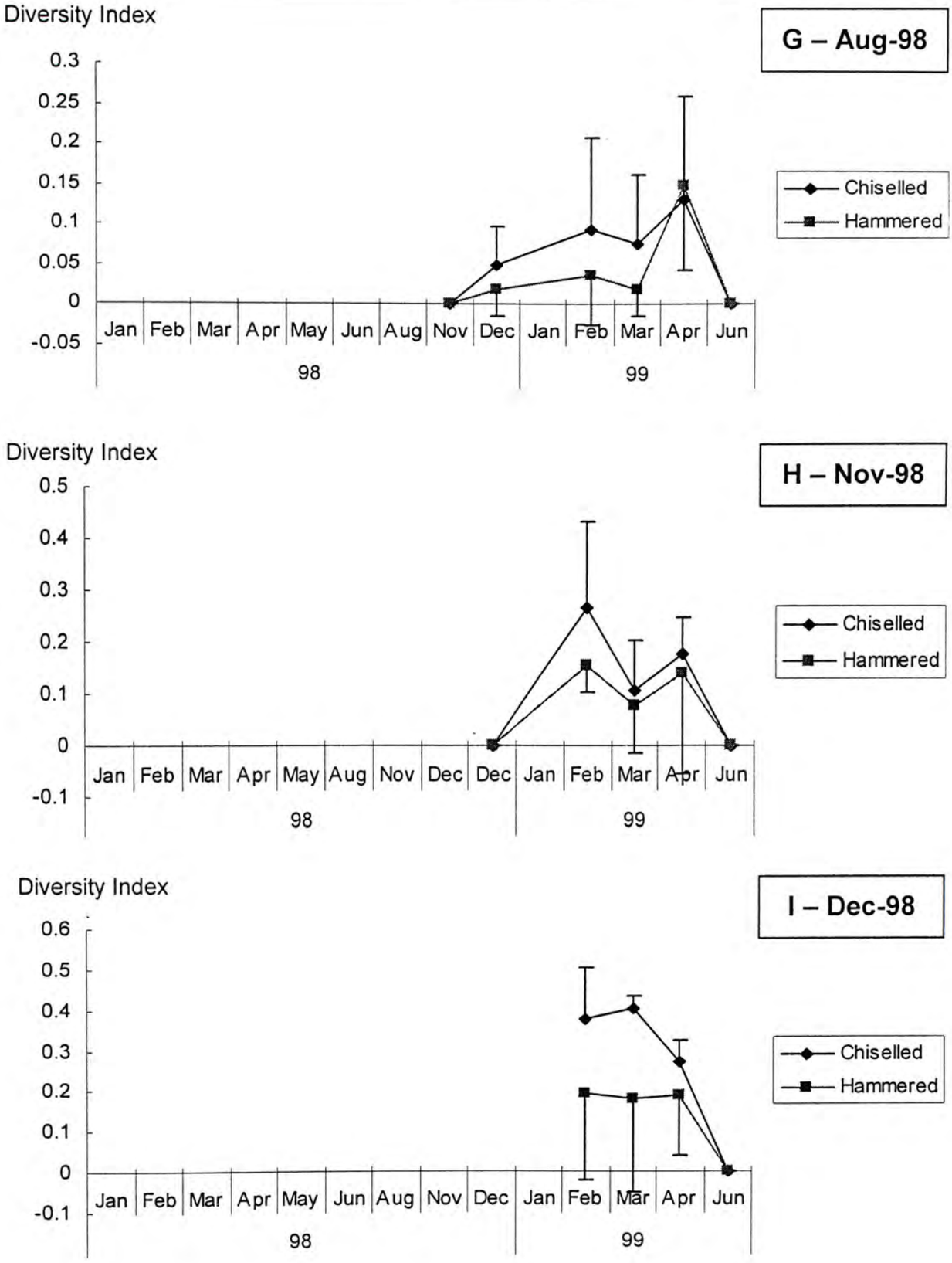


Fig. 3.5. Changes in mean species diversity (+/– SD) during subsequent months of observations in plots cleared at different times in A Ma Wan (Cont'd). (G) Aug-98 clearings, n = 3; (H) Nov-98 clearings, n = 3; (I) Dec-98 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

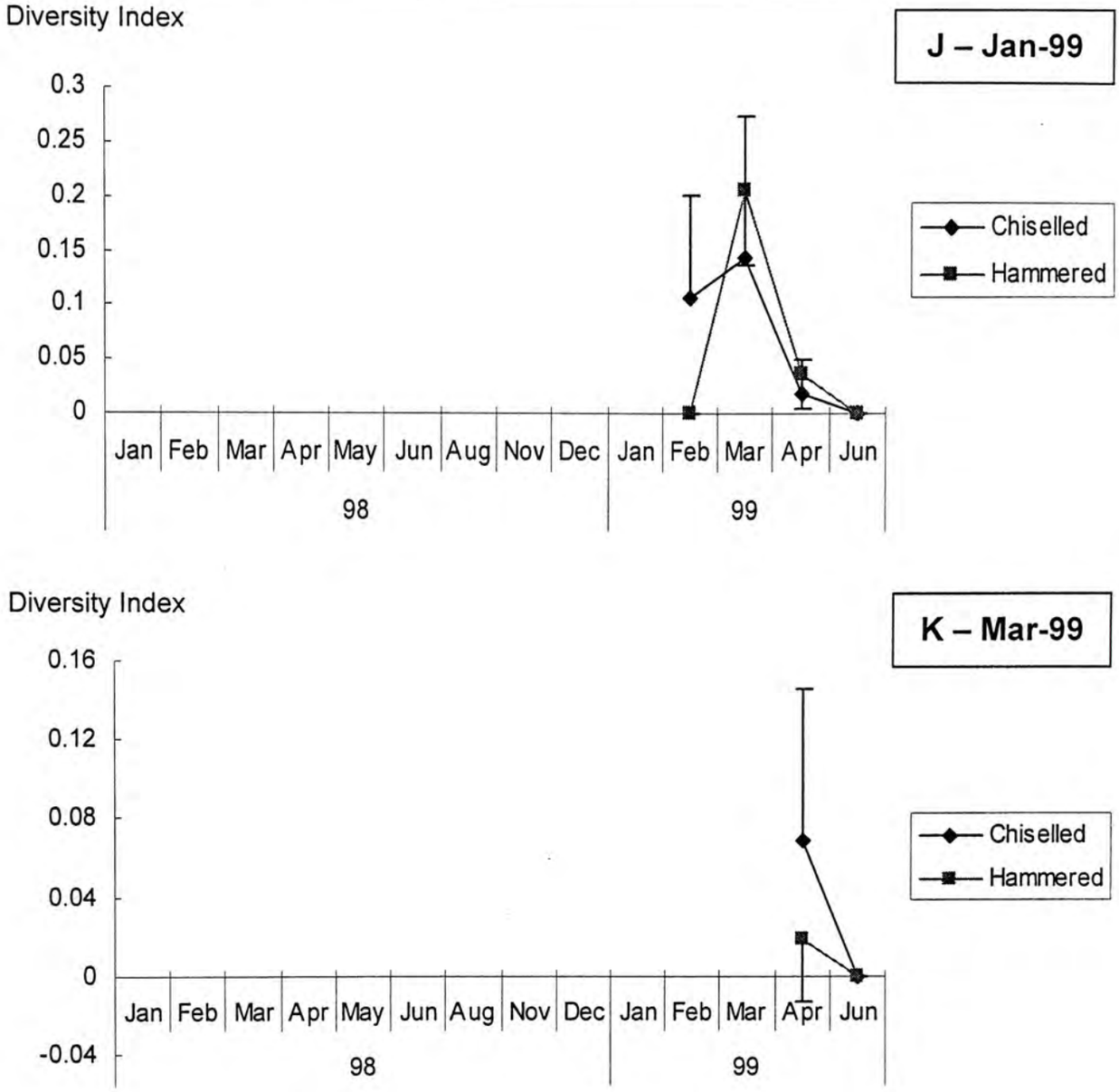


Fig. 3.5. Changes in mean species diversity (+/– SD) during subsequent months of observations in plots cleared at different times in A Ma Wan (Cont'd). (J) Jan-99 clearings, n = 3; (K) Mar-99 clearings, n = 3. No SD means that same number of species appeared in all the replicates.

# Chapter 4

# Colonization of Early Algal Assemblages on Artificial Substrata

## 4.1 Introduction

Setting up artificial substrata in the sea bottom has been of considerable interests for detailed examination of recruitment process in subtidal communities. These substrata allow one to investigate the dynamics of the algal recruits on a real bare surface. Yet, as suggested by Kennelly (1983), algal growth and recruitment patterns on artificial substrata have not usually been compared with those appeared on the surfaces which the settlement plates are supposed to represent – cleared patches on natural substrata.

Since the characteristics of marine hard substrata (e.g. surface texture, chemical composition and small-scale relief) can potentially influence the structure of attached epibenthic communities (Hixon & Brostoff 1985), the choice of materials that are used in a study could bias the information retrieved (Harlin & Lindbergh 1977). Due to this reason, some researchers carried out their trial experiments by using settlement plates made of different types of materials prior to selecting the most suitable one for their experiments (Adey & Vassar 1975, Neushul *et al.* 1976). Among various kinds of artificial substrata, plastic plates such as acrylic plates (Harlin & Lindbergh 1977, van Tamelen *et al.* 1997), Plexiglas plates (Neushul *et al.* 1976) and PVC plates (Adey & Vassar 1975, Hixon & Brostoff 1985, Leukart 1994, Kaehler & Williams 1997) were the most commonly used. Others like glass slides (Hruby & Norton 1979, Dion & Delepine 1983, Reed *et al.* 1988, Muñuz & Santelices 1994, Tyrrell & Johansen 1995), pottery tiles/bricks (Chapman 1984, Santos & Duarto 1996, Santelices & Varela 1994, van Tamelen *et al.* 1997), sandstone plates (Kennelly 1983), nylon lines (Deysher & Dean 1986), and concrete blocks/plates (Watanuki & Yamamoto 1990, Serisawa *et al.*

1998) were also chosen for algal recruitment studies. In order to allow the experimental substrata to have a much more similar textural finish as the natural substratum nearby, some researchers simply collected these substrata directly from the sea bottom *in situ* but processed them with some treatments. Examples could be seen in the use of sun-dried coralline rocks by Ang (1985), granite chips which were collected from the study site and cemented into small blocks by Ang (1991), bleached and sun-dried lava boulders by Kendrick (1991), sterilized valve fragments of the mussels by Santelices & Varela (1994) and also autoclaved Mactan stone blocks (made of coral stones) by Azanza-Corrales *et al.* (1996). In a study of thallus regeneration in *Solieria filiformis*, various types of natural and artificial substrata (some have just been mentioned above) were used in order to examine the ways by which the algal plants attached (Perrone & Cecere 1997). In the present study, ceramic tiles were chosen as the artificial substratum because they worked quite well in algal recruitment studies (Adey & Vassar 1975). Moreover, pottery had proved to be a good substratum for spore attachment (Santos & Duarte 1996, see also Hanic & Pringle 1978).

The previous field study of subtidal algal growth on artificial clearings (see Chapter 3) focused mainly on recruits which have grown for at least one month after settlement so that the algal recruits could be viewed macroscopically. Such study, however, provided no detailed examination about the patterns of early algal settlement (i.e. initial growth of the attached algae) (see also Kennelly 1983). Therefore, Kennelly (1983) suggested that microscopic sampling of settlement plates after two weeks of submersion in the field (i.e. biweekly-retrieved tiles) allowed an examination of early algal colonization. In this study, some ceramic tiles were collected one month after submersion (monthly-retrieved) and some were not collected until the end of the study period (permanently-placed) in addition to the biweekly-retrieved tiles. It is expected

that due to different lengths of submersion and times of retrieval of the ceramic tiles, different patterns of algal recruitment in a given time period could be observed and compared. Furthermore, possible mortality of recruits at any stage of growth and development could also be deduced from these three groups of recruitment tiles in Ping Chau.

## 4.2 Materials and Methods

### 4.2.1 Study sites

Algal recruitment in Ping Chau was studied by provision of artificial substrata from January 1998 to May 1999 in addition to setting up clearing areas on natural rock surface (see Chapter 3). This experiment was carried out in both A Ma Wan and Lung Lok Shui. In A Ma Wan, the experimental set-ups were placed at the sandy bottom in shallow water (−1 m CD), next to the siltstone terraces where the clearing plots were made. As described previously, there is an abundant growth of marine algae as well as populations of *Hypnea charoides* on these terraces during winter (see Chapters 2 & 3). Hence, algal propagules should be quite abundant particularly during the reproductive seasons of these marine algae. The growth and recruitment patterns of the recruited algae on these artificial substrata can thus provide some insights on the process of early algal colonization. In Lung Lok Shui, the experimental set-ups were placed at two different depths, −1 m CD and −2 to −3 m CD. The former is near the area where seasonal growth and reproduction of *H. charoides* were studied (see Chapter 2). The latter was chosen because of the presence of an algal zonation pattern away from the shore (personal observation). Therefore, it is possible that patterns of algal growth and recruitment on the settlement plates in deeper areas may differ from those collected in shallow water.

### 4.2.2 Experimental design

The artificial substrata used in this study were ceramic tiles (15.2 x 15.2 $cm^2$) with a smooth textural surface similar to the hammered plots of the natural substratum (see Chapter 3). A hole was drilled at the centre of the tiles so that they could be fixed onto bases made of stainless steel mesh using stainless steel screws and nuts. These bases, with three ceramic tiles fixed on top, were horizontally bolted onto a rectangular granite block (50 x 21 x 15 $cm^3$) (Fig. 4.1). The completed set-ups were then placed in the sea bottom at different sites (−1 m CD in A Ma Wan, −1 m CD and −2 to −3 m CD in Lung Lok Shui) by SCUBA diving.

Depending on the timing of retrieval, each tile in a set of three was designated as a biweekly-retrieved, monthly-retrieved and permanently-placed tile. Their respective position within the set was randomly chosen and is shown in Fig. 4.2. Four replicates were set up in each study site. The biweekly-retrieved tiles were removed and taken back to the laboratory for examination approximately once every two weeks (but once every month during summer and fall, from May to November in 1998) while the monthly-retrieved tiles were retrieved approximately once each month (but bimonthly during summer and fall, from May to November in 1998). New tiles were replaced each time. Due to occasional strong winds and/or monsoons, field trips were sometimes unsuccessful so that the tiles could not be retrieved exactly at a biweekly or monthly interval, particularly from December 1998 to February 1999. For the permanently-placed tiles, they were observed *in situ* but were not replaced with new tiles unless they were broken. They were retrieved and examined in the laboratory at the end of the study. During retrieval, tiles were removed from the set-up, bolted in pairs in between two pieces of stainless steel mesh (19 x 19 $cm^2$), and transported back to the laboratory. They were kept in seawater during transport.

### 4.2.3 Investigation for optimal sampling

The first batch of the biweekly-retrieved tiles in both A Ma Wan and Lung Lok Shui were treated as the trial run of the experiment. The purpose was to test if algae could be recruited onto the ceramic tiles and to provide a general idea on how organisms were recruited. Areas around the hole as well as near the four edges were not as flat as the rest of the tile surface. Hence, recruitment around these areas could be different from the rest of the flat surface due to some micro-conditions generated by unequal surfaces or edge effects. In order to prevent such influences from affecting the information on recruitment pattern, the areas around the hole and the four edges were not examined. Each tile was divided into four quadrants and an area of 5 x 5 $cm^2$ in size was examined with a quadrat.

The retrieved tiles (retrieved on 22 January 1998) were found to be evenly covered by a layer of small algal recruits. Due to their small sizes, they were observed with 80x to 120x magnification under the stereomicroscope. After several trials, they were found to be optimally counted within an area of 2 x 2 $mm^2$. Thus, the quadrat (5 x 5 $cm^2$) was equally divided into 625 small squares (2 x 2 $mm^2$ each) with an arrangement shown in Fig. 4.3. A general survey found that all retrieved tiles possessed similar algal species, which were evenly distributed on the surface. Thus, only three out of the 12 tiles in the first set-ups (four from –1 m CD in A Ma Wan, four from –1 m CD and –2 to –3 m CD in Lung Lok Shui) and three out of the four quadrants in each tile were haphazardly chosen for subsampling to find the minimum number of small squares to be counted in each quadrat to represent the abundance and diversity of algal recruits in each tile. Individuals of all algal species present on the 625 small squares of each quadrat were counted. The mean density, calculated as the mean number of individuals per small square (2 x 2 $mm^2$) in the three quadrats, was plotted against different number of

squares counted (Fig. 4.4). Mean density increased initially and leveled off at the point when about 180 squares were counted. To account for some counting errors, a total of 200 squares within one quadrat was determined as the minimum number of squares to be used in the subsampling. Using a random number table, the relative positions of these 200 squares were marked on the quadrat accordingly (Fig. 4.5).

### 4.2.4 Examination of tiles

Tiles were first recorded by an underwater video camera during each visit and the presence of grazers and other organisms was also recorded before the tiles were retrieved. For the biweekly- and monthly- retrieved tiles, they were examined under a stereomicroscope (80x to 120x in magnification) after being brought back to the laboratory. A quadrat (5 x 5 $cm^2$) with 200 random squares (2 x 2 $mm^2$ each) was used to examine the ceramic tiles. This quadrat, printed out on transparency films, was placed on top of one of the quadrants of the tile randomly chosen by a lottery draw. This was placed 1 cm away from the edge in order to eliminate the edge effects. Before examination, the tiles were rinsed very gently with filtered seawater using a soft brush to remove the sediments. This layer of sediments could also be further blown off for better observation with a plastic squeeze-bottle filled with filtered seawater. Under the stereomicroscope, different algal species were identified. Some recruits were picked out with the aid of a probe and mounted on a microslide for better observation under the microscope. The number of individuals of each algal species present on each random square of the quadrat was counted and recorded with a counter. During investigation, all the recruited tiles were submerged under filtered seawater in a bucket without a lid so that natural light and aeration could still be available to keep the recruited organisms alive. Since the tiles were not preserved with any chemicals, examination was usually completed within one week after retrieval. These recruited

tiles were replenished with fresh filtered seawater for nourishment periodically.

The algal recruits were investigated for their composition, species richness, mean density (excluding encrusting coralline algae whose percentage cover was presented instead) and species diversity (Brillouin's index).

#### 4.2.4.1 Species composition

Identification of species recruited onto the tiles was carried out under the stereomicroscope. As described above, a quadrat was placed over the tile and all species present in each small square of the quadrat were recorded. All algal species present in the biweekly-retrieved, monthly-retrieved and permanently-placed tiles were recorded respectively at each date of retrieval. Differences in species composition among these three types of tiles were compared.

#### 4.2.4.2 Species richness

The number of each algal species present in each small square of the quadrat on the ceramic tiles was counted and the mean number of algae in all the 200 squares within the quadrat represented the species richness of each tile. A mean number of species was obtained from the four replicates from each site. Algae that probably belonged to one or more species but could not be effectively distinguished from one another due to their small sizes were collectively grouped under a single category (e.g. filamentous green algae as "GF"). It was treated as a single species in all calculations for species richness and for all statistical analyses.

#### 4.2.4.3 Mean density

The mean density was calculated as the mean of the total number of individuals within

each small square (2 x 2 $mm^2$) of the quadrat. For recruits that appeared in patches, each patch was counted as one individual. However, encrusting coralline algae appeared in a rather large patch and thus they were excluded in the calculations of algal density for all tiles. Instead, their percentage cover was recorded and analyzed separately.

4.2.4.4 Percentage cover of encrusting coralline algae

The percentage cover of encrusting coralline algae was first estimated from each small square (2 x 2 $mm^2$) of the quadrat and the resultant percentage cover was obtained by calculating the mean of the 200 values for each tile.

4.2.4.5 Species diversity

The species diversity of each ceramic tile was calculated by Brillouin's Index of species diversity. The calculation is as follows:

$$H = (\log N! - \Sigma[\log n_i!])/N$$

where H = Brillouin's Index of species diversity of a single tile

$n_i$ = number of individuals of a given species present in a quadrat

N = total number of individuals (i.e. summation of number of individuals of all algal recruits in that quadrat)

4.2.5 Statistical analyses

Statistical analyses (SigmaStat, Jandel Scientific Software) were applied to further evaluate changes in all the variables under considerations: species richness, mean density, percentage cover of encrusting coralline algae and species diversity. Similar

to the clearing experiment in Chapter 3, data were first tested for normality by Kolmogorov-Smirnov test and homogeneity of variance by Levene Median test before the analyses. Where appropriate, the data were transformed by log (x + 1) or other methods (same as those used in clearing experiment) to meet the assumptions of parametric tests. However, despites all attempts on transformation, the parametric assumptions could not be met in all cases. Non-parametric analyses were then applied instead.

Kruskal Wallis One Way ANOVA on Ranks was used to evaluate changes in the variables for both biweekly- and monthly- retrieved tiles over time. All pairwise multiple comparisons were carried out by Dunn's Method. Mann-Whitney Rank Sum Test was applied to further evaluate the pairs that showed significant differences. Differences between the two groups of tiles were evaluated by Mann-Whitney Rank Sum Test.

### 4.3 Results

As described in Chapter 2, there are always severe waves and occasional strong monsoon in Lung Lok Shui (waves are much stronger in shallow water). The experimental set-ups at –1 m CD and –2 to –3 m CD were badly damaged in April and May 1998 respectively. New set-ups were placed in September 1998 but they were found completely destroyed again during the next visit to Lung Lok Shui at the end of that month. Thus, experiments in both areas had to be set up again in November 1998. Unfortunately, those at –1 m CD were all overturned and broken after two weeks. Therefore, this experiment effectively lasted only three months from January to March 1998. For those placed at –2 to –3 m CD, they were also entirely destroyed after 6 weeks. Thus, the experiments in Lung Lok Shui had to be terminated in January 1999.

Given that no meaningful information was obtained, only limited results from this part of the experiments are presented.

### 4.3.1 Species composition

Recruitment study on artificial substrata was carried out from January 1998 (first set-up of recruitment plates on 22-Jan 1998) to May 1999 (last retrieval on 29-May 1999) in both A Ma Wan and Lung Lok Shui. The small sizes of the algal recruits (< 1 mm in general) led to some difficulty in species identification. Almost all of them were just very young propagules so that no obvious features could be observed. Even with the aid of a probe, many of them were too soft to be picked out for mounting. As a result, algal recruits were subjectively identified and grouped according to their morphologies. Table 4.1 listed the algal groups present on the ceramic tiles in both A Ma Wan and Lung Lok Shui throughout the whole study period. Each group was named and abbreviated in accordance to its appearance and descriptions. Only few algal groups could show clear structures and were suspected to belong to a certain genus (e.g. "Am" – *Amphiroa*; "Cer" – *Ceramium*; "GB" – *Ulva*; "Lau" – *Laurencia*; "Sar" – *Sargassum*; "SpF" and "Sph" – *Sphacelaria*-liked filaments and propagules). The others were classified mainly by pigmentation (brown/green/red) and their structural features (in clumps, filamentous, in patches, blade-liked, fleshy, thin, uniseriate, etc.). These were the only information that could be used to classify the recruits.

### 4.3.2 A Ma Wan tiles

#### 4.3.2.1 Species richness

The mean number of species observed on the biweekly-retrieved tiles in A Ma Wan peaked on 22-Sep (6.3 ± 1.3) and 26-Nov (6.3 ± 2.1) in 1998 (Fig. 4.6A). Excluding

the two maxima, no obvious fluctuations were observed in 1998. A great drop in the mean number of species was found from 26-Nov 1998 to 17-Dec 1998 (2.0 ± 0.0), the lowest value recorded in 1998. This value then increased gradually to 5.0 ± 0.0 on 4-Mar, dropped slightly to 3.8 ± 1.0 on 25-Mar and rose again to 6.0 ± 0.8 on 11-May in 1999. The minimum value in 1999 was recorded on 29-May (2.0 ± 1.4).

The highest mean number of species on the monthly-retrieved tiles was found on 26-Nov 1998 (8.3 ± 2.2) (Fig. 4.6B). Similar to the biweekly-retrieved tiles, no obvious fluctuations were observed. The mean number of species ranged from 2.0 ± 0.0 on 29-May 1999 to 5.8 ± 3.0 on 22-Sep 1998, excluding the highest value recorded on 26-Nov 1998.

Statistical analyses showed that changes in the mean number of species were significantly different ($p < 0.05$) at different times for both biweekly- and monthly-retrieved tiles (see Appendix B Tables B1 & B2 for post-hoc tests). However, no significant differences ($p > 0.05$) were found in the mean number of species between these two types of tiles retrieved at the same date (Table 4.2).

4.3.2.2 Algal density

The mean density (ind. per 2 x 2 $mm^2$ square) of the biweekly-retrieved tiles was found to be quite low (< 25 ind. per square) in the first few months in 1998 (Fig. 4.7A). In late April, however, the value rose dramatically from 19.7 ± 9.8 ind. per square on 29-Apr to 130.8 ± 12.8 ind. per square on 19-May 1998. It remained at above 120 ind. per square until July, when it dropped suddenly from 142.8 ± 20.5 ind. per square (15-Jul) to 28.3 ± 3.1 ind. per square (20-Aug). The mean density did not increase thereafter except that a peak was observed on 26-Nov 1998 (148.0 ± 145.7 ind. per

square). On this date of retrieval, one of the four replicate tiles was found to recruit several thousands more individuals of the filamentous green (GF) than the others (Fig. 4.7A). Thus, a relatively large standard deviation was obtained. In 1999, the mean density was generally lower than 15 ind. per square.

For the monthly-retrieved tiles (Fig. 4.7B), only one sharp peak was observed in May (208.0 ± 17.6 ind. per square on 19-May) while a much smaller peak was observed in November 1998 (66.4 ± 19.0 ind. per square on 26-Nov). On other dates of retrieval, the mean algal density was less than 40 ind. per square in general.

Statistical analyses showed that changes in mean density on both biweekly- and monthly- retrieved tiles were significantly different ($p < 0.05$) over different dates of retrieval (see Appendix B Tables B3 & B4 for post-hoc tests). Within the same date of retrieval, mean algal density was not significantly different ($p > 0.05$) between the two types of tiles in most cases except during the period from 12-Mar 1998 to 15-Jul 1998 (Table 4.2).

Tables 4.3 A & B show the mean densities of different algal groups on the biweekly- and monthly- retrieved tiles in A Ma Wan at different dates of retrieval. On the biweekly-retrieved tiles (Table 4.3A), the mean density of the filamentous green (GF), ranging from 0.1 ± 0.1 ind. per square on 26-Mar 1998 to 139.0 ± 19.8 ind. per square on 15-Jul 1998 with particularly high values (> 100 ind. per square) recorded from May to July as well as in November 1998, was much higher than those of all the other groups of algae. The mean density of another green (green in patches, GP) was also relatively high, with maxima recorded on 26-Mar (14.0 ± 5.62 ind. per square) and 26-Nov (14.0 ± 4.8 ind. per square) in 1998. These two algal groups were found in all

seasons from the beginning to the end of the study period. Except for the brown (brown in patches, BP), whose mean density was recorded to be or exceeded 10 ind. per square on certain dates of retrieval (12-Mar, 26-Mar and 26-Nov in 1998), majority of the algal groups had a density that was less than 0.5 ind. per square at most of the dates of retrieval.

Similar to the biweekly-retrieved tiles, the mean density of the filamentous green (GF) present on the monthly-retrieved tiles in A Ma Wan was also much higher than those of the others. The maximum value (205.0 ± 18.7 ind. per square) was recorded on 19-May 1998 and it was the only group found in all seasons (Table 4.3B). The mean density of another green (green in patches, GP), which was not observed only on the last date of retrieval (29-May 1999), ranged from 2.0 ± 1.1 ind. per square on 15-Feb 1998 and 2.0 ± 1.8 ind. per square on 15-Jul 1998 to 14.0 ± 3.5 ind. per square on 12-Mar 1998. While for the brown (brown in patches, BP), a relatively high value (18.0 ± 5.1 ind. per square) was recorded on 12-Mar 1998. For the rest of the algal groups, the mean densities were mostly below 0.5 ind. per square in most of the dates of retrieval.

4.3.2.3 Percentage cover of encrusting coralline algae

The abundance of encrusting coralline algae on the tile was represented by their relative percentage cover. During the first few months of the study period (February to May 1998), the mean percentage cover of encrusting coralline algae on the biweekly-retrieved tiles in A Ma Wan remained extremely low, with coverage always less than 1 % (Fig. 4.8 A). The mean percentage was higher in late summer and fall (June to November 1998) than in the rest of the year. The value increased greatly from 3.0 ± 3.6 % on 20-Aug to a maximum of 29.0 ± 9.1 % in 29-Oct 1998 and then dropped to 2.8 ± 0.7 % on 26-Nov 1998. For the last few months (December 1998 to May 1999),

the mean value ranged only from 0.1 ± 0.1 % (22-Apr 1999) to 0.6 ± 0.3 % (11-May 1999). No encrusting coralline algae were recorded on the biweekly-retrieved tiles at dates 15-Feb, 26-Feb, 9-Apr, 17-Dec in 1998 and 25-Mar in 1999.

For the monthly-retrieved tiles, similar result was obtained (Fig. 4.8B). The mean values in percentage cover were very much higher during 15-Jul (46.1 ± 10.9 %), 22-Sep (55.6 ± 33.9 %) and 26-Nov 1998 (48.4 ± 30.0 %). On other dates of retrieval except 14-Jan 1999, less than 1 % of mean percentage cover was recorded. A cover of 1.7 ± 2.7 % was recorded on 14-Jan 1999. No encrusting coralline algae were observed on the monthly-retrieved tiles retrieved on 15-Feb and 9-Apr 1998.

Statistical analyses showed that changes in the percentage cover of encrusting coralline algae were significantly different ($p < 0.05$) during different dates of retrieval for both biweekly- and monthly- retrieved tiles (see Appendix B Tables B5 & B6 for post-hoc tests). However, no significant differences ($p > 0.05$) were found between these two types of tiles except on 15-Jul and 26-Nov in 1998 (Table 4.2).

#### 4.3.2.4 Species diversity

The pattern of changes in species diversity on biweekly-retrieved tiles appeared to be quite irregular (Fig. 4.9A). The mean value was recorded as 0.5 ± 0.1 on the first date of retrieval (15-Feb 1998) and it decreased gradually to 0.3 ± 0.0 on 26-Mar 1998. It then rose a little bit to 0.4 ± 0.0 (9-Apr 1998) and dropped very greatly to the second lowest point (< 0.1) on 19-May 1998. The diversity index remained below 0.1 until July, when it started to rise back to 0.3 ± 0.0 on 20-Aug 1998. After that, the index fluctuated around 0.2 until the end of the study period, when the value was below 0.1 (29-May 1999).

For the monthly-retrieved tiles (Fig. 4.9B), maximum values (> 0.4) were recorded in the first three dates of retrieval (15-Feb, 12-Mar and 9-Apr in 1998). The mean species diversity then dropped dramatically from the maximum (0.4 ± 0.0) on 9-Apr to less than 0.1 on 19-May 1998. It rose back to 0.4 ± 0.1 (22-Sep 1998) and fluctuated at around 0.3 thereafter. On the last date of retrieval (29-May 1999), the mean diversity index reached the second lowest value at 0.1 ± 0.1.

Statistical analyses showed that changes in the mean species diversity were significantly different ($p < 0.05$) among different dates of retrieval for both biweekly- and monthly- retrieved tiles (see Appendix B Tables B7 & B8 for post-hoc tests). However, no significant differences ($p > 0.05$) in species diversity were found between these two types of tiles at most of the dates of retrieval except on 12-Mar 1998, 15-Jul 1998 and 4-Mar 1999 (Table 4.2).

### 4.3.3 Lung Lok Shui tiles at –2 to –3 m CD – Biweekly-retrieved tiles

Due to strong waves, the tiles in Lung Lok Shui were frequently damaged or lost. As a result, only a very few points of data were obtained at both depths of –1 m CD and –2 to –3 m CD.

#### 4.3.3.1 Species richness

For Lung Lok Shui deep water tiles, a relatively high value of species richness on biweekly-retrieved tiles was recorded on 12-Mar 1998 (5.0 ± 1.0) (Fig. 4.10A). This value became lower in April (2.0 ± 0.0 on 29-Apr 1998). After several months, the species richness recorded was 2.0 ± 0.0 on 17-Dec 1998 and 2.8 ± 0.5 on 14-Jan 1999.

4.3.3.2 Algal density

The mean algal density of biweekly-retrieved tiles in Lung Lok Shui rose from 16.2 ± 6.6 ind. per 2 x 2 $mm^2$ square on 26-Feb 1998 to a relatively high value of 26.8 ± 7.7 ind. per square on 12-Mar 1998 (Fig. 4.10B). It then dropped gradually to 5.9 ± 1.4 ind. per square on 29-Apr 1998. The values recorded on 17-Dec 1998 and 14-Jan 1999 were 12.3 ± 1.9 ind. per square and 6.3 ± 2.5 ind. per square respectively.

Among these biweekly-retrieved tiles in Lung Lok Shui, the greens (filamentous, GF and green in patches, GP) were found at all dates of retrieval but the mean density of the filamentous green, with a relatively high value recorded on 17-Dec 1998 (6.4 ± 1.2 ind. per square), was comparatively lower than that recorded in A Ma Wan (Table 4.4 vs Table 4.3A). Green in patches (GP) showed relatively high densities, particularly on 12-Mar 1998 (22.0 ± 6.5 ind. per square). Except for BP (brown in patches), which had a density around 5 ind. per square on 12-Mar and 26-Mar in 1998, all the other groups of algae showed densities at values lower than 1 ind. per square in general.

4.3.3.3 Percentage cover of encrusting coralline algae

In Lung Lok Shui, less than 1 % cover of encrusting coralline algae was recorded on biweekly-retrieved tiles (Fig. 4.10C). The maximum percentage cover was found on 14-Jan 1999 (1.3 ± 2.5 %). No encrusting coralline algae were observed on tiles retrieved on 29-Apr and 17-Dec 1998.

4.3.3.4 Species diversity

The mean value of species diversity on biweekly-retrieved tiles rose gradually from 0.1 ± 0.1 on 26-Feb 1998 to a relatively high value of 0.3 ± 0.1 on 26-Mar 1998 (Fig. 4.10D). It then dropped slightly to 0.3 ± 0.0 on 29-Apr 1998. The mean diversity was

recorded as 0.3 ± 0.0 on 17-Dec 1998 and decreased slightly to 0.2 ± 0.0 on 14-Jan 1999.

Since only a few discontinuous data points were collected from the biweekly-retrieved tiles at –2 to –3 m CD in Lung Lok Shui, no significant trends could be determined from the above experimental results.

4.3.4 Lung Lok Shui tiles at –2 to –3 m CD – Monthly-retrieved tiles

For the monthly-retrieved tiles, there were 4.5 ± 1.3 species, 34.4 ± 5.6 ind. per 2 x 2 $mm^2$ square and a species diversity of 0.2 ± 0.1 recorded on 12-Mar 1998; 2.5 ± 0.6 species, 6.8 ± 2.0 ind. per square and a species diversity of 0.2 ± 0.1 recorded on 29-Apr 1998 and 3.5 ± 0.6 species, 3.4 ± 0.3 ind. per square and a diversity of 0.1 ± 0.0 recorded on 14-Jan 1999. No encrusting coralline algae were observed on these tiles. Other than these three dates of retrieval, no data were obtained for the monthly-retrieved tiles in deep water of Lung Lok Shui.

4.3.5 Lung Lok Shui tiles at –1 m CD

At the depth of –1 m CD in Lung Lok Shui, there were even less data collected for the biweekly- (on 26-Feb and 12-Mar in 1998) and monthly-retrieved (12-Mar 1998) tiles due to destruction of the experimental set-ups by strong wave action. On the biweekly-retrieved tiles, mean values for the different variables are: species richness, 3.5 ± 1.0 on 26-Feb and 5.0 ± 1.2 on 12-Mar, algal density, 12.8 ± 5.6 ind. per 2 x 2 $mm^2$ square on 26-Feb and 22.3 ± 7.4 ind. per square on 12-Mar and, species diversity, 0.2 ± 0.2 on 26-Feb and 0.3 ± 0.0 on 12-Mar.

For the monthly-retrieved tiles retrieved on 12-Mar 1998, the mean values of species

richness (4.8 ± 1.0) and diversity index (0.3 ± 0.1) were a bit lower than those recorded for the biweekly-retrieved tiles, whereas the mean algal density was relatively higher (35.2 ± 6.9 ind. per square). No encrusting coralline algae were observed on both types of tiles at −1 m CD in Lung Lok Shui. Species like filamentous brown (BF), brown patches (BP), filamentous green (GF) and green patches (GP) were recorded on both types of tiles while green blades (GB) and filamentous red (RF) were found only on biweekly-retrieved tiles and brown clumps (BC) and red patches (RP), on monthly-retrieved tiles. The BP (brown in patches) at 2.0 ± 2.6 ind. per square on 26-Feb and 10.0 ± 5.3 ind. per square on 12-Mar in 1998 for the biweekly-retrieved tiles and 11.2 ± 5.5 ind. per square on 12-Mar 1998 for the monthly-retrieved tiles, and the GP (green in patches) at 10.3 ± 2.2 ind. per square on 26-Feb and 12.3 ± 4.3 ind. per square on 12-Mar in 1998 for the biweekly-retrieved tiles and 23.7 ± 5.2 ind. per square on 12-Mar in 1998 for the monthly-retrieved tiles, showed higher densities than the others. The mean densities of most other algal species were less than 1 ind. per square.

### 4.3.6 Permanently-placed tiles in A Ma Wan and Lung Lok Shui

The permanently-placed tiles in both A Ma Wan and Lung Lok Shui were examined and the species recruited on these tiles were recorded during each visit. It was found that encrusting brown algae, which were most frequently found throughout the study period (Table 4.5), started to recruit as many tiny dots on the tiles in A Ma Wan in February and grew denser in April 1998 (Fig. 4.11A). In June, no obvious algal recruits were observed except for encrusting coralline algae, which became the most dominant in July and August (Table 4.5). A layer of filamentous green algae covered all the tiles in September and October but encrusting brown and coralline algae dominated the tiles again starting from October (Fig. 4.11 B). In November 1998,

about 20 *Sargassum* recruits were observed and one of them grew up to a length of 10 cm in March 1999 (Fig. 4.11C). Its maximum length was recorded to be 17.5 cm on 22-Apr 1999. Several *Sargassum* recruits started to die back in February 1999 (9-Feb 1999) but three of them persisted until the end of the study. Recruits of *Hypnea charoides* were not found throughout the study period. However, after the placement of an extra granite block with tiles which were transferred from Lung Lok Shui (after the destruction of experimental set-ups due to strong waves), some recruits were found and appeared like *Hypnea* (Fig. 4.11D). Since the tiles were originally from Lung Lok Shui, it was not sure where exactly these recruits came from. These two recruits grew for only two months and disappeared in May 1999. After retrieval, the permanently-placed tiles were observed under the stereomicroscope in the laboratory and all the algal recruits observed were more or less the same as those recorded *in situ*, except that a suspected *Laurencia* recruit was observed (Table 4.5).

On the permanently-placed tiles at −2 to −3 m CD in Lung Lok Shui, recruits of *Colpomenia sinuosa* were first recorded on 12-Mar 1998 and they grew quickly and covered the entire tile on 26-Mar 1998 (Fig. 4.11E). Also, there were many small clumps of filamentous green algae observed in March and April in 1998 and also in January 1999 (Fig. 4.11F). This observation was quite different from that recorded in A Ma Wan, where encrusting brown and coralline algae were the dominant species on the tiles within that period of time (but not in January 1999) (Table 4.5). No data were obtained for those tiles placed at −1 m CD in Lung Lok Shui.

### 4.3.7 Presence of grazers and other organisms

During the *in situ* observation on the ceramic tiles, the presence of grazers and other organisms were recorded. In A Ma Wan, *Chlorostoma rustica* and *Pyrene* spp. were

most commonly found among all the molluscs observed (Table 4.6). Other species were also recorded but they were collectively classified as bivalves, cowries (*Cypraea arabicus*), limpets (including *Cellana* spp. and *Patelloida* spp.) and other gastropods (excluding bivalves and limpets; including top shells like *Astraea rhodostoma* and *Monodonta* spp.; turban shells like *Lunella* spp. and *Turbo* spp.; winkles and periwinkles like *Nodilittorina* spp. and *Littorina* spp.; mitres like *Mitra* sp. and others like *Nerita* spp. and *Siphonaria* spp.). Other organisms such as tubeworms, nudibranchs, sea anemones, sea urchins, barnacles (*Tetraclita squamosa*) and hermit crabs were also recorded. In Lung Lok Shui (at depths of –1 m CD and –2 to –3 m CD), similar organisms were observed, such as *Chlorostoma rustica*, *Pyrene* spp., hermit crabs and fish (*Siganus canaliculatus*).

## 4.4 Discussion

In A Ma Wan, algal recruits were found on the ceramic tiles throughout the whole study period (22-Jan 1998 to 29-May 1999). Most of these recruits were of small sizes, including those from the monthly-retrieved or permanently-placed tiles. The latter should have been in the water for a long period enough for the recruits to grow but it was found that only few recruits grew to a detectable size. Based on their different sizes, the algal recruits could be generally divided into micro- and macro- recruits. According to Ang (1991), microrecruits, which are < 1 mm and are not normally visible to the unaided eyes, are germlings developed from fertilized eggs recently discharged (i.e. within 1 month). Macrorecruits are > 1 mm long and can be detected by the unaided eyes. They are those that developed from eggs discharged at least 3 or 4 months earlier (Ang 1991). In the present study, the definitions of these two types of recruits can be modified slightly. Microrecruits may be referred to the germlings developed from fertilized eggs or spores discharged within 2 weeks time while

macrorecruits are those developed from eggs or spores discharged approximately one month earlier.

The introduction of biweekly-retrieved tiles in this experiment focused on the recruitment patterns of microrecruits in a short period of time, whereas the monthly-retrieved tiles could capture both micro- and macro- recruits within a one-month interval. The permanently-placed tiles were aimed at monitoring the survival of any algal recruits during the study period. Significant differences in all the variables examined (i.e. species richness, mean density, percentage cover of encrusting coralline algae and species diversity) in biweekly- and monthly- retrieved tiles over time indicated that there were temporal variations in recruitment patterns.

Although algal recruits were observed throughout the year, relatively high number of species was recorded from mid to late fall (22-Sep 1998 and 26-Nov 1998 on biweekly-retrieved tiles, 26-Nov 1998 on monthly-retrieved tiles), indicating that more propagules from different algal species were available during that period of time (Fig. 4.6). In the Galapagos archipelago, Kendrick (1991) found that there was a strong seasonality in species richness, more species occurring during the "Garua" season (August to November) than the "El Niño" season (December to July). Furthermore, periodic surveys by Neushul *et al.* (1976) showed that high recruitment rates for plants generally resulted in the summer and summer-installed plates supporting significantly different populations at the end of the experimental period (12 months) from the winter-installed plates. Temporal variation in algal recruitment is also well documented by other workers (Harlin & Lindbergh 1977, Deysher & Norton 1982, Reed *et al.* 1988, Ang 1991). It is mostly agreed that the main factor which determines whether a species appears on the shore or not is the availability of

propagules from fertile parent plants (Harlin & Lindbergh 1977, Hruby & Norton 1979, Deysher & Norton 1982, Ang 1991, Santos & Duarte 1996, Kaehler & Williams 1997). This implies that, to a certain extent, recruitment seasonality is related to reproductive seasonality of the algae.

Peak recruitment of algal recruits in A Ma Wan was observed in summer (19-May to 15-Jul in 1998) and late fall (26-Nov 1998) on both types of tiles (Fig. 4.7). These, respectively, are the periods after and before the growing season of most marine algae every year in A Ma Wan (see Chapter 2). The peak observed in summer might be due to the many marine algae becoming fertile at the end of the growing season in spring, thus increasing the availability of propagules. A great drop in algal density observed from July to August in 1998 might be due to the growth of encrusting coralline algae, which showed their peak recruitment in September and October 1998 (Fig. 4.8). They could potentially inhibit the growth of other algae. Another peak of algal recruitment, however, was observed after the summer die-off (i.e. before the growing season) when there were no obvious marine algae observed in A Ma Wan (see Chapter 3). This suggested that algal spores or propagules might not all recruit immediately on the rocky substratum after they were released. Instead, they existed as some microscopic floating forms in the water column during summer and fall and settled as recruits only when the conditions became favourable (i.e. late fall to winter). The present result thus supports the suggestions from related studies on reproductive seasonality of *Hypnea charoides* (see Chapter 2) and algal recruitment on artificial clearings (see Chapter 3) that floating forms of algal spores or propagules in A Ma Wan could persist in the water column through the adverse conditions in summer and germinate into adult plants when the conditions are more favourable. In a population of *Fucus distichus*, Ang (1991) observed that macrorecruits appeared continuously even after a

period of absence in mircorecruits and suggested that this continuous presence of macrorecruits might be due to the existence of a "germling bank" of microrecruits, which survived for a prolonged period and grew to a detectable size only when conditions became favourable. In the present study, the continuous presence of algal recruits throughout the study period and the presence of a sharp peak recorded on both biweekly- and monthly- retrieved tiles after summer die-off suggested an existence of a similar "germling bank", most likely in microscopic floating forms.

In contrast to the mean density, obvious minima were observed in species diversity (19-May and 15-Jul in 1998), i.e. when the mean density was the highest for both biweekly- and monthly- retrieved tiles, implying that the recruitment tiles were dominated by only one or two algal species during that period of time. These dominant species were the green algae, filamentous green (GF) and the green in patches (GP) (Table 4.3). The density of these two algal species affected much the variations in both diversity index and the overall mean density of all algae as they had the largest number of individuals recruited on the tile. In Academy Bay of Galapagos archipelago, Kendrick (1991) showed that the patchiness of marine algal communities in shallow tropical reefs was partly determined by patterns of recruitment of the two component species, i.e. crustose coralline and filamentous turf algal communities. This suggested that, in the present case, the filamentous green and the green in patches might be the component species in structuring the recruitment patterns of the early algal assemblages in A Ma Wan. Another possibility that leads to the dominance of these green algae might be the nature of ephemeral algae, which have the ability to settle on a newly opened space quickly, precluding the growth of other algal species at times (Hruby & Norton 1979, Chapman 1984, Kendrick 1991, Serisawa *et al.* 1998, see also Chapter 3).

The overall recruitment patterns of both biweekly- and monthly- retrieved tiles in terms of species richness, mean density, percentage cover of encrusting coralline algae and species diversity appeared to be similar to each other, in which they rose and fell nearly at the same time. Statistical analyses further showed that there were no obvious significant differences between these two types of tiles at any time of a year with respect to all the variables investigated. However, significant difference between different dates of retrieval indicates that the time when the tiles were placed in the water was more important than the length of time that they were immersed in the water.

The monthly-retrieved tiles were found mostly covered by microrecruits (personal observation), though they were supposed to capture both micro- and macro- recruits. These indicated that the microrecruits recorded on the tiles did not all successfully develop into macrorecruits after two weeks of growth, suggesting large mortality of the algal recruits during the recruitment process. The generally high values recorded on monthly-retrieved tiles in terms of all the variables investigated might be mainly due to a longer time for recruitment.

The absence of adult plants observed on the permanently-placed tiles also showed that only minority of the recruits were able to grow into detectable size. One exception was that a layer of filamentous green algae was found in September and October in 1998 (personal observation), i.e. two months after the end of the first peak of recruitment in biweekly-retrieved tiles (15-Jul 1998), indicating that some algal recruits (particularly the filamentous green) did survive and develop into the adult population. Nevertheless, this adult population lasted only for about one month and exhibited another mortality thereafter, which might be due to the inhibition of growth

by the presence and dominance of encrusting brown and coralline algae starting from October 1998 (Table 4.11). In the *Sargassum* beds in Western Australia, Kendrick & Walker (1994) found that 43 % of the adult plants were successfully developed from recruits. In contrast, Ang (1991) found that in *Fucus distichus*, the peak of macro-recruitment did not always follow that of micro-recruitment, suggesting a differential survivorship of microrecruits at different times. Reed (1990) also showed that strong density-dependent mortality occurred whenever there was recruitment, even though high number of sporophyte recruits was a result of great spore density. High mortality of recruits, as was suggested from the present results, appears to be a common phenomenon among algae. However, many marine algae were found successfully developed from propagules in the hammered plots of the clearing experiment (see Chapter 3). One possibility may be the differential nature and texture between a natural substratum and an artificial substratum and hence, the choice of substrata may also be a factor that affected algal recruitment. It thus would be wise in general for researchers to use settling plates as natural as possible in any benthic study (Harlin & Lindbergh 1977, Hixon & Brostoff 1985, Santelices 1990).

The critical algal recruitment period in A Ma Wan was most likely from mid to late fall (October and November), i.e. before the growing season of most marine algae. This is evidenced by the observation on the permanently-placed tiles, in which more adult plants were observed during the algal growing season (from December 1998 to May 1999) (Table 4.5). However, relatively few species were found in the growth period in 1998. One possibility is that the experimental tiles were placed in the water in January 1998 and missed the peak recruitment period in the previous fall (i.e. in 1997). More evidently, *Sargassum* recruits were not observed in early 1998 but were recorded simultaneously on the three types of experimental tiles in November 1998 (Tables 4.3

& 4.5). This strongly suggests that late fall is the most critical period for the recruitment of *Sargassum* in A Ma Wan.

The major differences between the results obtained in Lung Lok Shui (mainly from tiles at depths of –2 to –3 m CD) and those from A Ma Wan were that overall values in Lung Lok Shui were slightly lower than those from A Ma Wan in terms of species richness and diversity, and much lower in terms of mean density and percentage cover of encrusting coralline algae (Fig. 4.10 & Table 4.4). This general decrease in the values of all variables could be explained by the influence of strong waves, which resulted in high water flow, on recruitment. According to van Tamelen *et al.* (1997), a negative correlation between algal settlement and water flow in the field might be that high water flow could inhibit the release of propagules and their settlement, or might be detrimental to propagules immediately after settlement (see also Norton & Fetter 1981, Serrao *et al.* 1996). Strong water currents could also carry spores away to the open sea and cause dislodgement of sporelings, resulting in high mortality rates of algae (Azanza-Corrales *et al.* 1996). These suggest that spatial variation may exist between the two study sites, which can be caused by the differences in physical environments. Another obvious difference between Lung Lok Shui and A Ma Wan was that the permanently-placed tiles in the former were fully covered by recruits of *Colpomenia sinuosa* in March 1998 and many clumps of filamentous green algae were observed in March and April in 1998 (Figs. 4.11 E & F), suggesting a rapid growth as well as a successful survival of certain algal recruits under such a strong wave condition. These recruits were completely absent in A Ma Wan at those periods of time, further indicating a spatial variation in algal recruits between the two places. Though frequent damage of experimental set-ups due to strong waves resulted in insufficient data to determine any trends and patterns of algal recruitment in Lung Lok

Shui, the few undamaged tiles still showed that a number of algae were able to recruit onto them successfully (e.g. filamentous green, *C. sinuosa*, *Sargassum* and *Sphacelaria*).

Table 4.1. Abbreviations used to represent different algal groups present on ceramic tiles placed in both A Ma Wan and Lung Lok Shui and their descriptions.

| Algal groups | Descriptions |
|---|---|
| **Am** | Suspected *Amphiroa*, few branches observed |
| **BC** | Brown, appeared in clumps |
| **BF** | Brown, filamentous, appeared singly |
| **rBF** | Reddish brown, filamentous, appeared singly |
| **BP** | Brown, appeared in patches |
| **dBP** | Brown, appeared in patches but seemed to be made up of tiny dots |
| **enC** | Encrusting coralline algae |
| **Cer** | Suspected *Ceramium* |
| **DF** | Dark, filamentous, appeared singly |
| **GB** | Green, appeared in blades (suspected *Ulva*) |
| **GF** | Green, filamentous, appeared singly |
| **tGF** | Green, filamentous, very thin, appeared singly |
| **GP** | Green, appeared in patches |
| **Lau** | Suspected *Laurencia* |
| **RB** | Red, fleshy and a bit cylindrical, appeared in blades |
| **RF** | Red, filamentous, appeared singly |
| **cRF** | Red, filamentous, appeared in clusters |
| **fRF** | Red, filamentous, appeared singly, fleshy |
| **tRF** | Red, filamentous, very thin, appeared singly |
| **uRF** | Red, filamentous, uniseriate (clearly seen) , appeared singly |
| **RP** | Red, appeared in patches |
| **Sar** | *Sargassum* spp. |
| **SpF** | *Sphacelaria*-liked filaments |
| **Sph** | *Sphacelaria* propagules (structure clearly seen) |

Table 4.2. Results of Mann-Whitney Rank Sum Test comparing the species richness, mean density, percentage cover of encrusting coralline algae (ECA) and species diversity between biweekly- and monthly- retrieved tiles in A Ma Wan retrieved on the same date from 15-Feb 1998 to 29-May 1999. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Date of Retrieval | | Species Richness | Mean Density | Percentage Cover (ECA) | Species Diversity |
|---|---|---|---|---|---|
| 1998 | 15-Feb | (no difference) | 0.2000 | (no difference) | 0.3429 |
| | 12-Mar | 0.6857 | 0.0286* | 0.4857 | 0.0286* |
| | 9-Apr | 0.6857 | 0.0286* | (no difference) | 0.6857 |
| | 19-May | 0.6857 | 0.0286* | 0.2000 | 0.1143 |
| | 15-Jul | 0.8824 | 0.0286* | 0.0286* | 0.0286* |
| | 22-Sep | 0.4857 | 0.8857 | 0.3429 | 0.8857 |
| | 26-Nov | 0.2000 | 0.3429 | 0.0286 | 0.4857 |
| 1999 | 14-Jan | 0.2000 | 0.1143 | 0.2000 | 0.3429 |
| | 4-Mar | 0.1143 | 0.6857 | 0.3429 | 0.0286* |
| | 22-Apr | 0.8857 | 0.4857 | 0.8857 | 0.8857 |
| | 29-May | 0.6286 | 0.8597 | 0.8571 | 0.8571 |

Table 4.3A. Mean densities (number of individuals per 2 x 2 $mm^2$ square) (± SD) of different algal groups on biweekly-retrieved tiles in A Ma Wan at different dates of retrieval from 15 February 1998 to 29 May 1999 (n = 4; n = 3 on 20-Aug 1998). Refer to Table 4.1 for the list of abbreviations.

| Algal groups | 1998 15/2 | 26/2 | 12/3 | 26/3 | 9/4 | 29/4 | 19/5 | 15/6 | 15/7 | 20/8 | 22/9 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BF | 0.2 ± 0.2 | 0.4 ± 0.2 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| rBF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 |
| BP | 1.0 ± 0.7 | < 0.01 | 12.0 ± 4.4 | 10.0 ± 1.6 | 3.0 ± 0.6 | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | < 0.1 |
| DF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.0 ± 2.2 |
| GB | 0 | 0 | < 0.01 | < 0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GF | 3.0 ± 0.6 | 4.0 ± 0.4 | 0.3 ± 0.4 | 0.1 ± 0.1 | 2.0 ± 0.6 | 14.0 ± 7.2 | 130.0 ± 12.4 | 126.0 ± 8.5 | 139.0 ± 19.8 | 19.0 ± 4.4 | 27.0 ± 9.1 |
| GP | 3.0 ± 1.2 | 6.0 ± 0.6 | 11.0 ± 2.1 | 14.0 ± 5.6 | 5.0 ± 1.4 | 6.0 ± 2.6 | 1.0 ± 0.5 | 4.0 ± 2.0 | 3.0 ± 1.5 | 9.0 ± 1.3 | 10.0 ± 2.7 |
| RB | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 | 0 |
| RF | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 ± 0.4 |
| tRF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 |
| RP | 0 | 0 | 0 | 0 | < 0.01 | 0 | < 0.01 | < 0.01 | 0 | < 0.1 | < 0.01 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SpF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | < 0.01 |
| Sph | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 4.3A. Mean densities (number of individuals per 2 x 2 $mm^2$ square) (± SD) of different algal groups on biweekly-retrieved tiles in A Ma Wan at different dates of retrieval from 15 February 1998 to 29 May 1999 (n = 4; n = 3 on 20-Aug 1998) (Cont'd). Refer to Table 4.1 for the list of abbreviations.

| Algal groups | 1998 | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 29/10 | 26/11 | 17/12 | 14/1 | 9/2 | 4/3 | 25/3 | 22/4 | 11/5 | 29/5 |
| BF | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | < 0.01 | < 0.01 |
| rBF | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 |
| BP | 0 | 10.0 ± 6.8 | 0 | 0 | 0.4 ± 0.18 | 2.0 ± 1.4 | 0 | 0.1 ± 0.1 | 0.1 ± 0.1 | 0 |
| DF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GB | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GF | 36.0 ± 3.6 | 125.0 ± 148.3 | 21.0 ± 15.4 | 6.0 ± 3.0 | 0.4 ± 0.1 | 0.2 ± 0.0 | 2.1 ± 0.4 | 4.0 ± 2.4 | 5.0 ± 2.9 | 2.0 ± 2.4 |
| GP | 3.0 ± 0.5 | 14.0 ± 4.8 | 6.0 ± 3.9 | 6.0 ± 3.0 | 8.0 ± 3.0 | 4.0 ± 1.8 | 4.0 ± 0.3 | 3.0 ± 0.5 | 6.0 ± 1.8 | < 0.01 |
| RB | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 |
| RF | < 0.1 | < 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 |
| tRF | < 0.01 | < 0.1 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 |
| RP | < 0.01 | < 0.01 | 0 | 0 | 0 | < 0.1 | < 0.1 | < 0.1 | 0.1 ± 0.0 | 0 |
| Sar | 0 | < 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SpF | < 0.01 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 | < 0.01 | < 0.01 | < 0.01 | 0 |
| Sph | 0 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 |

Table 4.3B. Mean densities (number of individuals per 2 x 2 $mm^2$ square) (± SD) of different algal groups on monthly-retrieved tiles in A Ma Wan at different dates of retrieval from 15 February 1998 to 29 May 1999 (n = 4; n = 3 on 29-May 1999). Refer to Table 4.1 for the list of abbreviations.

| Algal | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| groups | 15/2 | 12/3 | 9/4 | 19/5 | 15/7 | 22/9 | 26/11 | 14/1 | 4/3 | 22/4 | 29/5 |
| Am | 0 | 0 | 0 | 0 | 0 | < 0.01 | < 0.01 | 0 | 0 | 0 | 0 |
| BF | < 0.1 | < 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BP | 3.0 ± 1.6 | 18.0 ± 5.1 | 5.0 ± 0.9 | 0 | 0 | 0 | 2.0 ± 2.9 | 0 | 1.0 ± 0.8 | 0.2 ± 0.2 | 0 |
| dBP | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 |
| Cer | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 | 0 |
| DF | 0 | 0 | 0 | 0 | < 0.01 | 4.0 ± 4.7 | 0 | 0 | 0 | 0 | 0 |
| GF | 6.0 ± 3.3 | 5.0 ± 2.7 | 12.0 ± 2.8 | 205.0 ± 18.7 | 4.0 ± 2.7 | 22.0 ± 9.8 | 58.0 ± 19.4 | 2.0 ± 1.5 | < 0.1 | 2.0 ± 2.0 | 2.0 ± 2.1 |
| tGF | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 |
| GP | 2.0 ± 1.1 | 14.0 ± 3.5 | 9.0 ± 3.2 | 3.0 ± 1.2 | 2.0 ± 1.8 | 7.0 ± 1.0 | 6.0 ± 1.4 | 5.0 ± 1.4 | 4.0 ± 0.7 | 3.0 ± 0.9 | 0 |
| Lau | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 | 0 |
| RF | 0 | < 0.01 | 0 | 0 | 0 | 1.0 ± 0.7 | 0.4 ± 0.7 | 0 | < 0.01 | 0 | 0 |
| cRF | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 | 0 |
| fRF | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 |
| tRF | 0 | 0 | 0 | 0 | 0 | 0.2 ± 0.3 | 0 | 0 | 0 | 0 | 0 |
| uRF | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 |
| RP | 0 | 0 | 0 | < 0.01 | < 0.1 | 0 | < 0.1 | < 0.01 | 0 | < 0.1 | < 0.01 |
| Sar | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 | 0 | 0 | 0 |
| SpF | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 |
| Sph | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | < 0.01 | 0 |

Table 4.4. Mean densities (number of individuals per 2 x 2 $mm^2$ square) (± SD) of different algal groups on biweekly-retrieved tiles at –2 to –3 m CD in Lung Lok Shui at different dates of retrieval from 26 February 1998 to 14 January 1999 (n = 4; n = 3 on 12- & 26- Mar 1999). Refer to Table 4.1 for the list of abbreviations.

| Algal groups | 1998 26/2 | 12/3 | 26/3 | 9/4 | 17/12 | 1999 14/1 |
|---|---|---|---|---|---|---|
| **BF** | 0.1 ± 0.0 | 0.1 ± 0.1 | 0 | 0 | 0 | 0 |
| **BP** | 1.0 ±1.2 | 4.9 ± 1.0 | 5.4 ± 1.8 | 0 | 0 | < 0.01 |
| **GB** | 0 | < 0.1 | 0 | 0 | 0 | 0 |
| **GF** | < 0.1 | < 0.1 | 0.4 ± 0.2 | 2.8 ± 1.7 | 6.4 ± 1.2 | 1.4 ± 0.5 |
| **GP** | 15.0 ± 5.5 | 22.0 ± 6.5 | 14.0 ± 7.5 | 3.1 ± 0.8 | 5.9 ± 1.3 | 4.9 ± 2.0 |
| **RF** | < 0.01 | 0 | 0 | 0 | 0 | 0 |

Table 4.5. Occurrence of different algal groups (indicated by "×") on permanently-placed tiles observed *in situ* at different dates (= retrieval dates of biweekly- and monthly- retrieved tiles from 22-Jan 1998 to 29-May 1999) and in laboratory after retrieval ("Lab Obs" – "Laboratory Observation"). These tiles were located in A Ma Wan and Lung Lok Shui. ("enB" – "encrusting brown algae"; "unB" – "unknown brown"; "Col" – "*Colpomenia sinuosa*"; "Hyp" – "suspected *Hypnea*"; "cR" – "red, creeping"; "unR" – "unknown red"; "Ul" – "Ulva"; others refer to Table 4.1 for the list of abbreviations.)

| | | Site Observation | | | | | | | | | | | | | | | | | | | | | Lab |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1998 | | | | | | | | | | | | | | 1999 | | | | | | | Obs |
| Site | Groups | 22/1 | 15/2 | 26/2 | 12/3 | 26/3 | 9/4 | 29/4 | 19/5 | 15/6 | 15/7 | 20/8 | 22/9 | 29/10 | 26/11 | 17/12 | 14/1 | 9/2 | 4/3 | 24/3 | 22/4 | 11/5 | 29/5 | 29/5 |
| A Ma Wan | BP | | | | | | | | | | | | | | | | | | | | | | | × |
| | enB | | × | × | × | × | × | × | × | × | | | | × | × | × | × | × | × | × | × | × | × | × |
| | unB | | | | | | × | | | | | | | | | | | | | | | | | |
| | enC | | | | × | | | × | | × | × | × | × | × | × | × | × | × | | | | | | × |
| | GF | | | | | | × | × | | | | | × | × | | | × | | | | | | | × |
| | Hyp | | | | | | | | | | | | | | | × | | | | × | × | | | |
| | Lau | | | | | | | | | | | | | | | | | | | | | | | × |
| | cR | | | | | | | | | | | | | | | | × | | × | × | × | × | × | |
| | fR | | | | × | | × | | | | | | | × | | | | | | | × | | | × |
| | Sar | | | | | | | | | | | | | | × | × | × | × | × | × | × | × | × | × |
| | Ul | | | | | | | × | | | | | | | | | | | | | | | | |
| Lung Lok Shui | enB | | | | | × | | × | | | | | | | | | | | | | | | | |
| | enC | | | | | × | | | | | | | | | | × | | | | | | | | |
| | Col | | | | × | × | | | | | | | | | | | | | | | | | | |
| | GF | | | | × | × | | × | | | | | | | | × | × | | | | | | | |
| | unR | | | | | | | × | | | | | | | | | | | | | | | | |

Table 4.6. Different kinds of grazers and other organisms recorded on biweekly-retrieved, monthly-retrieved and permanently-placed tiles in A Ma Wan from February 1998 to May 1999.

| Date of Observation | Biweekly-retrieved | Monthly-retrieved | Permanently-placed |
|---|---|---|---|
| 15.02.98 | | *Chlorostoma rustica* | *Chlorostoma rustica* |
| 26.02.98 | *Pyrene* spp. | *Pyrene* spp. | *Chlorostoma rustica* |
| | | | Hermit crabs |
| | | | Limpets |
| | | | Tubeworms |
| 12.03.98 | Hermit crabs | Limpets | *Chlorostoma rustica* |
| | Other gastropods | | Limpets |
| | | | Tubeworms |
| 26.03.98 | | | Limpets |
| | | | Tubeworms |
| 09.04.98 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | | *Pyrene* spp. | *Pyrene* spp. |
| | | Sea urchins | Limpets |
| | | | Tubeworms |
| 29.04.98 | *Chlorostoma rustica* | *Pyrene* spp. | *Pyrene* spp. |
| | Limpets | | Limpets |
| | Tubeworms | | Tubeworms |

Table 4.6. Different kinds of grazers and other organisms recorded on biweekly-retrieved, monthly-retrieved and permanently-placed tiles in A Ma Wan from February 1998 to May 1999 (Cont'd).

| Date of Observation | Biweekly-retrieved | Monthly-retrieved | Permanently-placed |
|---|---|---|---|
| 19.05.98 | *Pyrene* spp. | *Chlorostoma rustica* | *Pyrene* spp. |
| | | *Pyrene* spp. | Hermit crabs |
| | | | Limpets |
| | | | Tubeworms |
| 15.06.98 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Pyrene* spp. |
| | *Pyrene* spp. | *Pyrene* spp. | Limpets |
| | | Hermit crabs | Tubeworms |
| 15.07.98 | Hermit crabs | *Chlorostoma rustica* | Hermit crabs |
| | | *Pyrene* spp. | Limpets |
| | | Other gastropods | |
| 20.08.98 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | *Pyrene* spp. | *Pyrene* spp. | *Pyrene* spp. |
| | | Hermit crabs | |
| 22.09.98 | *Cypraea arabicus* | Crabs | |
| 29.10.98 | *Tetraclita squamosa* | *Tetraclita squamosa* | Other gastropods |
| | | | Tubeworms |
| 26.11.98 | *Pyrene* spp. | *Chlorostoma rustica* | |
| | Limpets | *Pyrene* spp. | |

Table 4.6. Different kinds of grazers and other organisms recorded on biweekly-retrieved, monthly-retrieved and permanently-placed tiles in A Ma Wan from February 1998 to May 1999 (Cont'd).

| Date of Observation | Biweekly-retrieved | Monthly-retrieved | Permanently-placed |
|---|---|---|---|
| 17.12.98 | *Chlorostoma rustica* | *Chlorostoma rustica* | |
| | *Pyrene* spp. | *Pyrene* spp. | |
| | Other gastropods | Other gastropods | |
| 14.01.99 | Limpets | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | | *Pyrene* spp. | Limpets |
| | | Bivalves | Tubeworms |
| | | Limpets | |
| 09.02.99 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | Limpets | *Pyrene* spp. | Limpets |
| | | Hermit crabs | Other gastropods |
| | | Limpets | Nudibranchs |
| 04.03.99 | *Chlorostoma rustica* | *Pyrene* spp. | *Chlorostoma rustica* |
| | Limpets | Limpets | Limpets |
| | | Tubeworms | Sea urchins |
| 24.03.99 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | *Pyrene* spp. | *Pyrene* spp. | *Pyrene* spp. |
| | Limpets | Hermit crabs | Limpets |
| | | Limpets | Tubeworms |

Table 4.6. Different kinds of grazers and other organisms recorded on biweekly-retrieved, monthly-retrieved and permanently-placed tiles in A Ma Wan from February 1998 to May 1999 (Cont'd).

| Date of Observation | Biweekly-retrieved | Monthly-retrieved | Permanently-placed |
|---|---|---|---|
| 22.04.99 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | Limpets | Limpets | *Pyrene* spp. |
| | | Sea anemones | Limpets |
| 11.05.99 | *Chlorostoma rustica* | *Chlorostoma rustica* | *Chlorostoma rustica* |
| | *Pyrene* spp. | *Pyrene* spp. | *Pyrene* spp. |
| | Limpets | Limpets | Hermit crabs |
| | | | Limpets |
| | | | Sea anemones |
| 29.05.99 | *Chlorostoma rustica* | *Tetraclita squamosa* | *Chlorostoma rustica* |
| | *Pyrene* spp. | Limpets | Limpets |
| | Limpets | | |
| | Sea anemones | | |

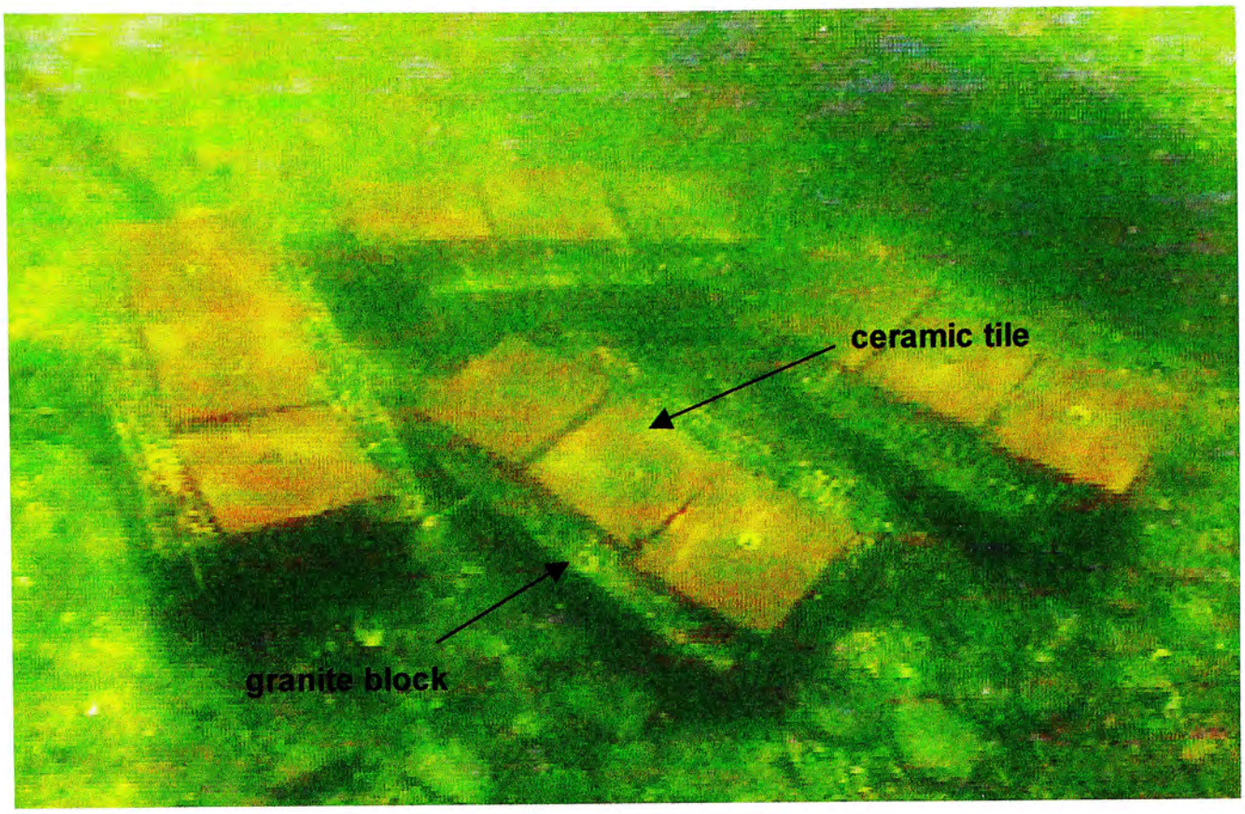


Fig. 4.1. Experimental set-up. Granite blocks with three ceramic tiles horizontally bolted on the top.

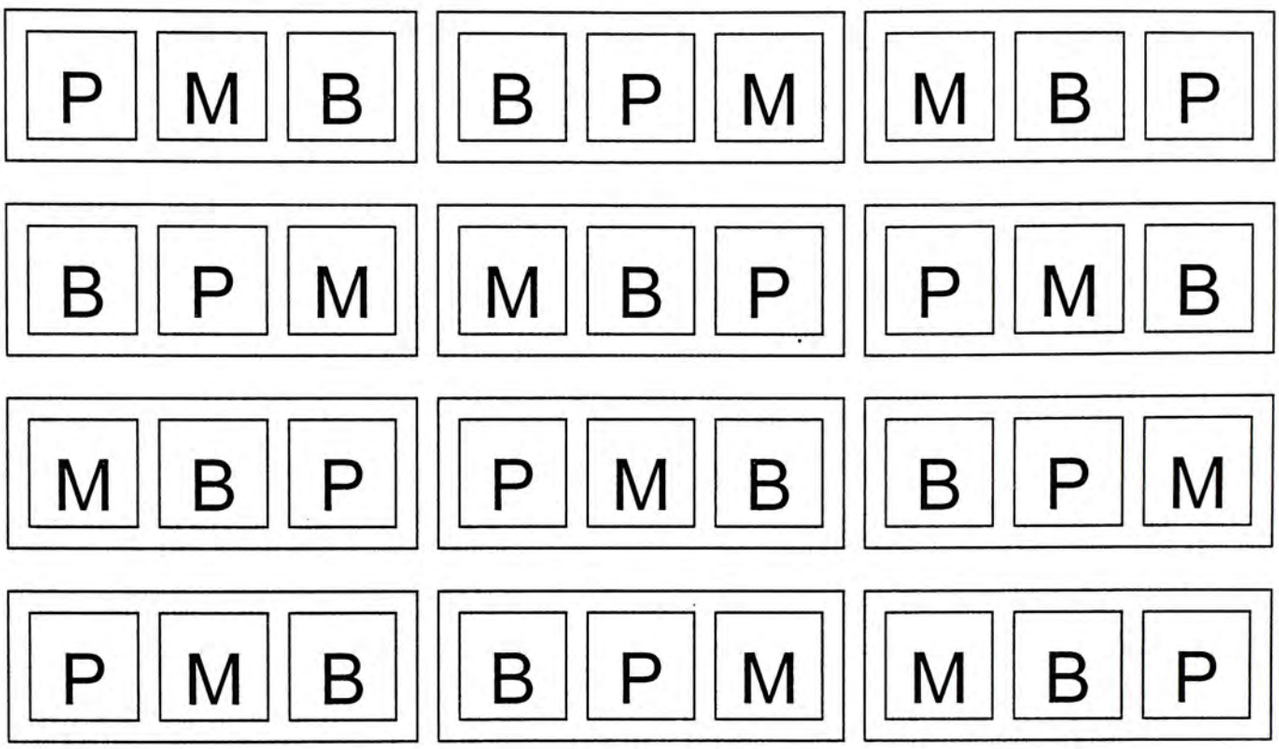


Fig. 4.2. Arrangement of tiles. Arrangement of biweekly-retrieved (B), monthly-retrieved (M) and permanently-placed (P) tiles on the four granite blocks in A Ma Wan (–1 m CD) and Lung Lok Shui (–1 m CD and –1 to –2 m CD).

| 1 | 26 | 51 | 76 | 101 | 126 | 151 | 176 | 201 | 226 | 251 | 276 | 301 | 326 | 351 | 376 | 401 | 426 | 451 | 476 | 501 | 526 | 551 | 576 | 601 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | 27 | 52 | 77 | 102 | 127 | 152 | 177 | 202 | 227 | 252 | 277 | 302 | 327 | 352 | 377 | 402 | 427 | 452 | 477 | 502 | 527 | 552 | 577 | 602 |
| 3 | 28 | 53 | 78 | 103 | 128 | 153 | 178 | 203 | 228 | 253 | 278 | 303 | 328 | 353 | 378 | 403 | 428 | 453 | 478 | 503 | 528 | 553 | 578 | 603 |
| 4 | 29 | 54 | 79 | 104 | 129 | 154 | 179 | 204 | 229 | 254 | 279 | 304 | 329 | 354 | 379 | 404 | 429 | 454 | 479 | 504 | 529 | 554 | 579 | 604 |
| 5 | 30 | 55 | 80 | 105 | 130 | 155 | 180 | 205 | 230 | 255 | 280 | 305 | 330 | 355 | 380 | 405 | 430 | 455 | 480 | 505 | 530 | 555 | 580 | 605 |
| 6 | 31 | 56 | 81 | 106 | 131 | 156 | 181 | 206 | 231 | 256 | 281 | 306 | 331 | 356 | 381 | 406 | 431 | 456 | 481 | 506 | 531 | 556 | 581 | 606 |
| 7 | 32 | 57 | 82 | 107 | 132 | 157 | 182 | 207 | 232 | 257 | 282 | 307 | 332 | 357 | 382 | 407 | 432 | 457 | 482 | 507 | 532 | 557 | 582 | 607 |
| 8 | 33 | 58 | 83 | 108 | 133 | 158 | 183 | 208 | 233 | 258 | 283 | 308 | 333 | 358 | 383 | 408 | 433 | 458 | 483 | 508 | 533 | 558 | 583 | 608 |
| 9 | 34 | 59 | 84 | 109 | 134 | 159 | 184 | 209 | 234 | 259 | 284 | 309 | 334 | 359 | 384 | 409 | 434 | 459 | 484 | 509 | 534 | 559 | 584 | 609 |
| 10 | 35 | 60 | 85 | 110 | 135 | 160 | 185 | 210 | 235 | 260 | 285 | 310 | 335 | 360 | 385 | 410 | 435 | 460 | 485 | 510 | 535 | 560 | 585 | 610 |
| 11 | 36 | 61 | 86 | 111 | 136 | 161 | 186 | 211 | 236 | 261 | 286 | 311 | 336 | 361 | 386 | 411 | 436 | 461 | 486 | 511 | 536 | 561 | 586 | 611 |
| 12 | 37 | 62 | 87 | 112 | 137 | 162 | 187 | 212 | 237 | 262 | 287 | 312 | 337 | 362 | 387 | 412 | 437 | 462 | 487 | 512 | 537 | 562 | 587 | 612 |
| 13 | 38 | 63 | 88 | 113 | 138 | 163 | 188 | 213 | 238 | 263 | 288 | 313 | 338 | 363 | 388 | 413 | 438 | 463 | 488 | 513 | 538 | 563 | 588 | 613 |
| 14 | 39 | 64 | 89 | 114 | 139 | 164 | 189 | 214 | 239 | 264 | 289 | 314 | 339 | 364 | 389 | 414 | 439 | 464 | 489 | 514 | 539 | 564 | 589 | 614 |
| 15 | 40 | 65 | 90 | 115 | 140 | 165 | 190 | 215 | 240 | 265 | 290 | 315 | 340 | 365 | 390 | 415 | 440 | 465 | 490 | 515 | 540 | 565 | 590 | 615 |
| 16 | 41 | 66 | 91 | 116 | 141 | 166 | 191 | 216 | 241 | 266 | 291 | 316 | 341 | 366 | 391 | 416 | 441 | 466 | 491 | 516 | 541 | 566 | 591 | 616 |
| 17 | 42 | 67 | 92 | 117 | 142 | 167 | 192 | 217 | 242 | 267 | 292 | 317 | 342 | 367 | 392 | 417 | 442 | 467 | 492 | 517 | 542 | 567 | 592 | 617 |
| 18 | 43 | 68 | 93 | 118 | 143 | 168 | 193 | 218 | 243 | 268 | 293 | 318 | 343 | 368 | 393 | 418 | 443 | 468 | 493 | 518 | 543 | 568 | 593 | 618 |
| 19 | 44 | 69 | 94 | 119 | 144 | 169 | 194 | 219 | 244 | 269 | 294 | 319 | 344 | 369 | 394 | 419 | 444 | 469 | 494 | 519 | 544 | 569 | 594 | 619 |
| 20 | 45 | 70 | 95 | 120 | 145 | 170 | 195 | 220 | 245 | 270 | 295 | 320 | 345 | 370 | 395 | 420 | 445 | 470 | 495 | 520 | 545 | 570 | 595 | 620 |
| 21 | 46 | 71 | 96 | 121 | 146 | 171 | 196 | 221 | 246 | 271 | 296 | 321 | 346 | 371 | 396 | 421 | 446 | 471 | 496 | 521 | 546 | 571 | 596 | 621 |
| 22 | 47 | 72 | 97 | 122 | 147 | 172 | 197 | 222 | 247 | 272 | 297 | 322 | 347 | 372 | 397 | 422 | 447 | 472 | 497 | 522 | 547 | 572 | 597 | 622 |
| 23 | 48 | 73 | 98 | 123 | 148 | 173 | 198 | 223 | 248 | 273 | 298 | 323 | 348 | 373 | 398 | 423 | 448 | 473 | 498 | 523 | 548 | 573 | 598 | 623 |
| 24 | 49 | 74 | 99 | 124 | 149 | 174 | 199 | 224 | 249 | 274 | 299 | 324 | 349 | 374 | 399 | 424 | 449 | 474 | 499 | 524 | 549 | 574 | 599 | 624 |
| 25 | 50 | 75 | 100 | 125 | 150 | 175 | 200 | 225 | 250 | 275 | 300 | 325 | 350 | 375 | 400 | 425 | 450 | 475 | 500 | 525 | 550 | 575 | 600 | 625 |

Fig. 4.3. Arrangement of squares. Arrangement of the 625 small squares (2 x 2 $mm^2$ each) of the quadrat (5 x 5 $cm^2$) used in the initial investigation for the mean number of squares needed to obtain a representative information on algal abundance and diversity in the recruitment tiles.

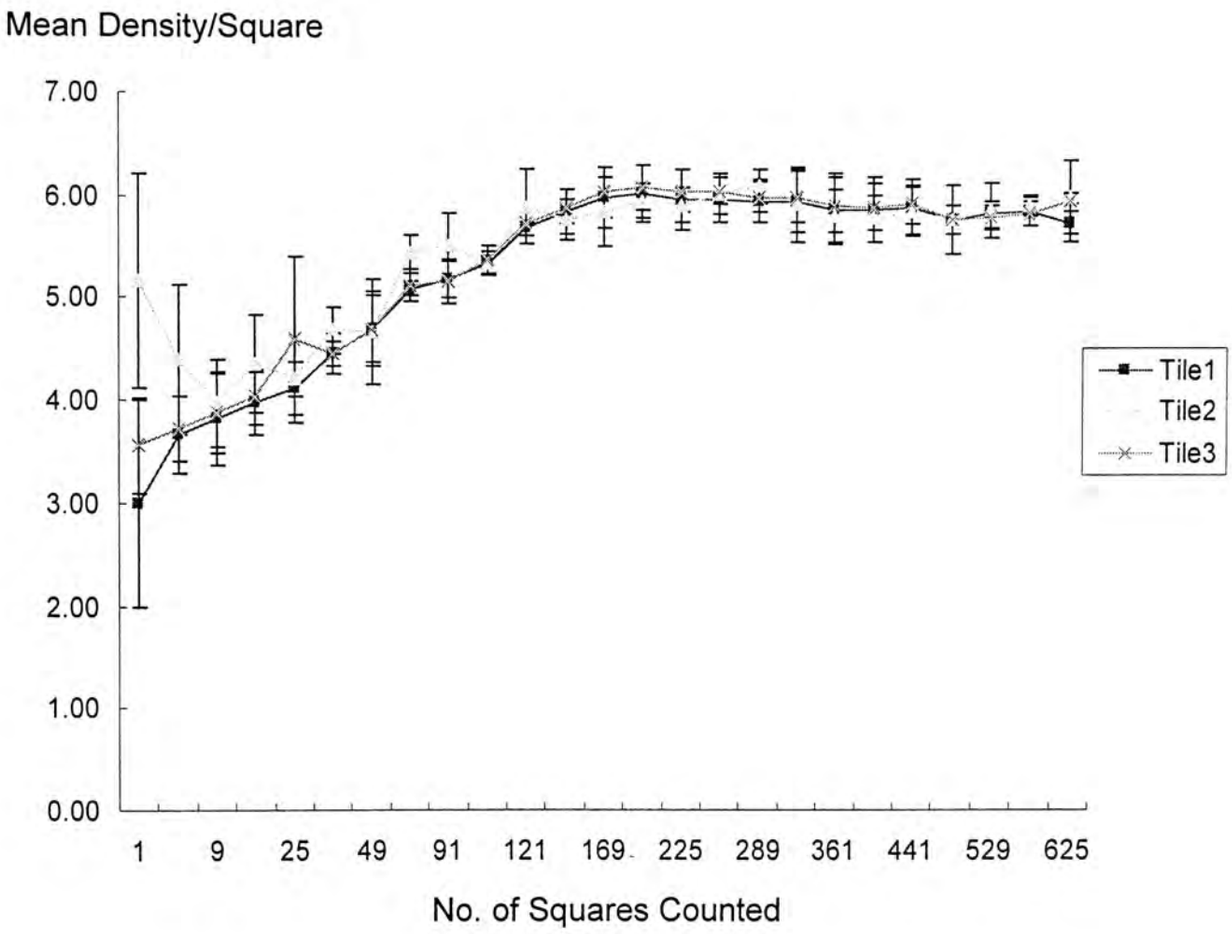


Fig. 4.4. Mean density. Mean density (total number of individuals per 2 x 2 $mm^2$ square) (± SD) of the three chosen tiles against different number of squares counted on the quadrat.

| 1 | | 51 | | 101 | | | | 201 | 226 | 251 | | | | | 376 | 401 | | 451 | 476 | | 526 | 551 | | 601 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | 202 | | 252 | 277 | | | 352 | | 402 | 427 | 452 | | | | | | |
| | | | | | 128 | 153 | | | | 253 | | 303 | | | | 403 | 428 | | | 503 | | | | |
| | 29 | 54 | 79 | | | | | | 229 | | | | | 354 | 379 | | | | 479 | | 529 | | | |
| 5 | | 55 | 80 | | | | 180 | | | | | | | | | | 430 | | 480 | 505 | 530 | | 580 | |
| | | | | | 131 | | | | | | | | 331 | | | 406 | | | | | 531 | 556 | | |
| | 32 | | | | | 157 | 182 | | | | | | | 357 | 382 | | | 457 | 482 | 507 | | 557 | | |
| | | | | | | | | 208 | | | 283 | | 333 | | | | 433 | | 483 | | 533 | 558 | | 608 |
| | | 59 | 84 | | | | | | | | | | | 359 | | | | 459 | | 509 | | | | |
| | | | | | 135 | | | 210 | 235 | | | 310 | 335 | 360 | | 410 | | 460 | | 510 | 535 | | | |
| | | | 86 | | | | 186 | 211 | 236 | | 286 | | | | | | 436 | | | | | 561 | 586 | 611 |
| | 37 | | | | | 162 | | | 237 | | | | | | | | | 462 | | | | | 587 | |
| 13 | | 63 | | | | | | 213 | | | 288 | | 338 | | | 413 | | | 488 | 513 | | 563 | 588 | |
| 14 | | 64 | | | 139 | | | | | | | 314 | | | 389 | | | 464 | 489 | 514 | | 564 | | |
| 15 | 40 | | | | 140 | | 190 | | 240 | | | | | | 390 | | | | | | | | | |
| | 41 | | | | | | | | 241 | | | | | 366 | | | 441 | | | | 541 | | 591 | 616 |
| | | | | | | | 192 | | | | | | 342 | 367 | | 417 | | 467 | | 517 | | | | |
| | | | | 118 | 143 | | | | 243 | | | | | 368 | | | | 468 | 493 | | 543 | 568 | | |
| 19 | 44 | | | | 144 | | | | 244 | | 294 | 319 | 344 | 369 | | | | | | | | | | |
| 20 | | | | | 145 | | 195 | | | 270 | | 320 | | | | 420 | | | | 520 | 545 | | 595 | 620 |
| 21 | | 71 | | | | | | | 246 | | | 321 | 346 | | | | | 471 | | | | 571 | | 621 |
| | | 72 | | | | | | | 247 | | 297 | | | | 397 | | | | | | | 572 | | |
| | 48 | | 98 | | | | | | | | | 323 | | | | | | | 498 | 523 | 548 | | 598 | 623 |
| | | 74 | | | | | 199 | | 249 | | | | | 374 | | 424 | | | 499 | 524 | | 574 | 599 | |
| | 50 | | 100 | 125 | | | | 225 | | 275 | | 325 | | 375 | | | | 475 | | | | 575 | 600 | 625 |

Fig. 4.5. Arrangement of squares. Arrangement of the 200 random squares (2 x 2 $mm^2$ each) of the quadrat (5 x 5 $cm^2$) used in the examination of the ceramic tiles.

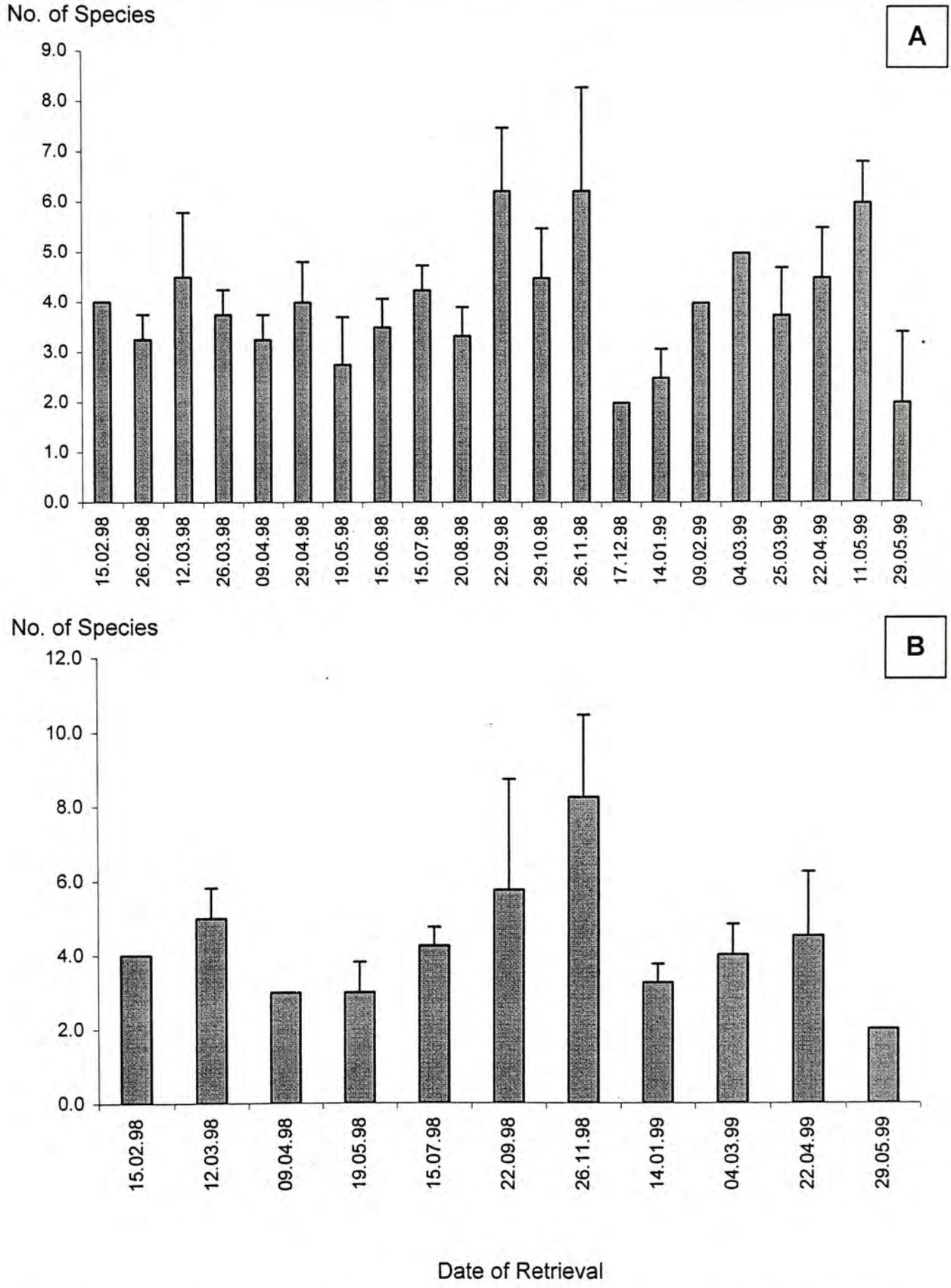


Fig. 4.6. Species richness. Changes in mean number of species (+ SD, n = 4; n = 3 on 20-Aug 1998 for biweekly-retrieved tiles and on 29-May 1999 for monthly-retrieved tiles) on (A) biweekly- and (B) monthly-retrieved tiles in A Ma Wan from 15-Feb 1998 to 29-May 1999.

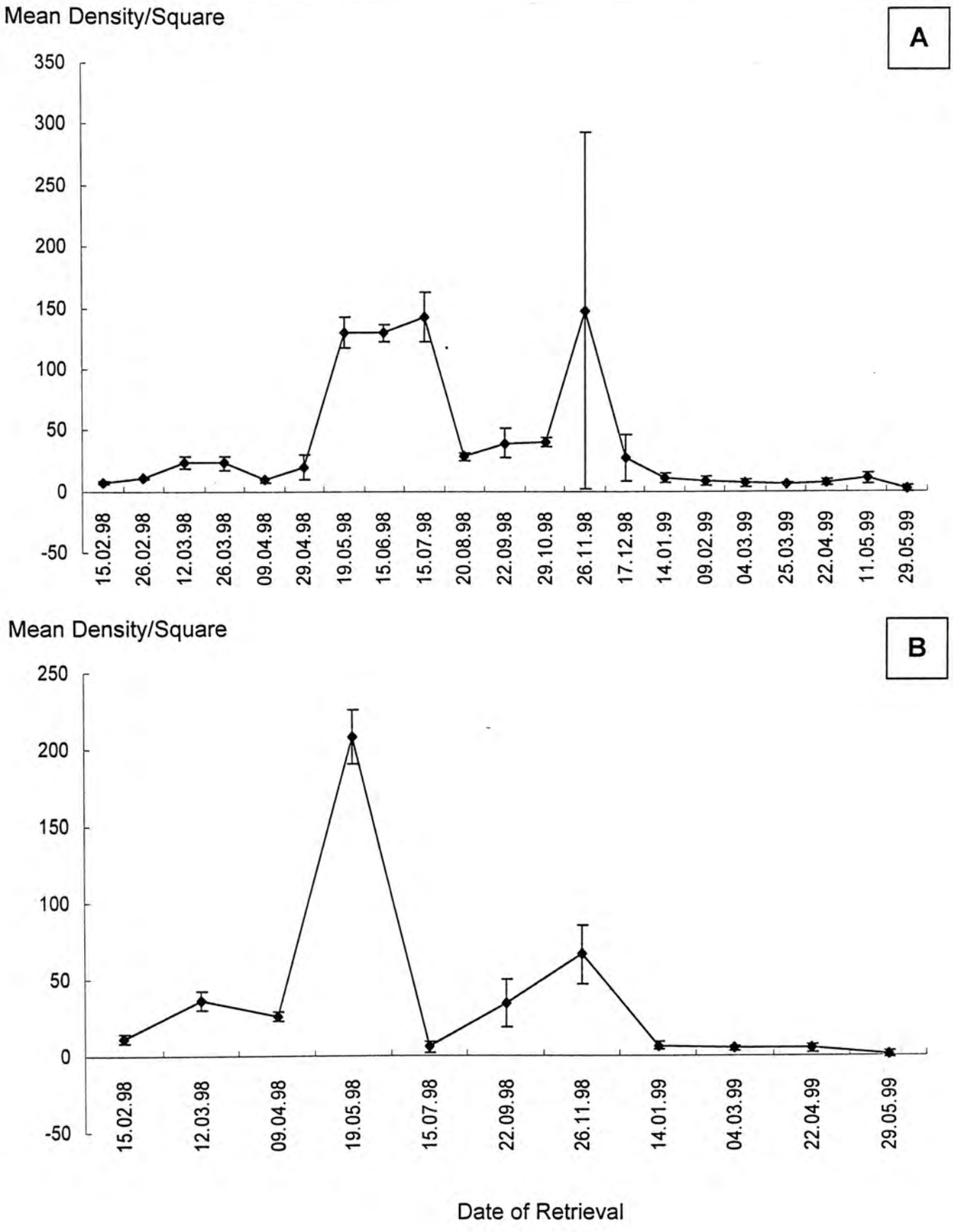


Fig. 4.7. Mean density. Changes in mean density (total number of individuals per 2 x 2 $mm^2$ square) (± SD, n = 4; n = 3 on 20-Aug 1998 for biweekly-retrieved tiles and on 29-May 1999 for monthly-retrieved tiles) on (A) biweekly- and (B) monthly-retrieved tiles in A Ma Wan from 15-Feb 1998 to 29-May 1999.

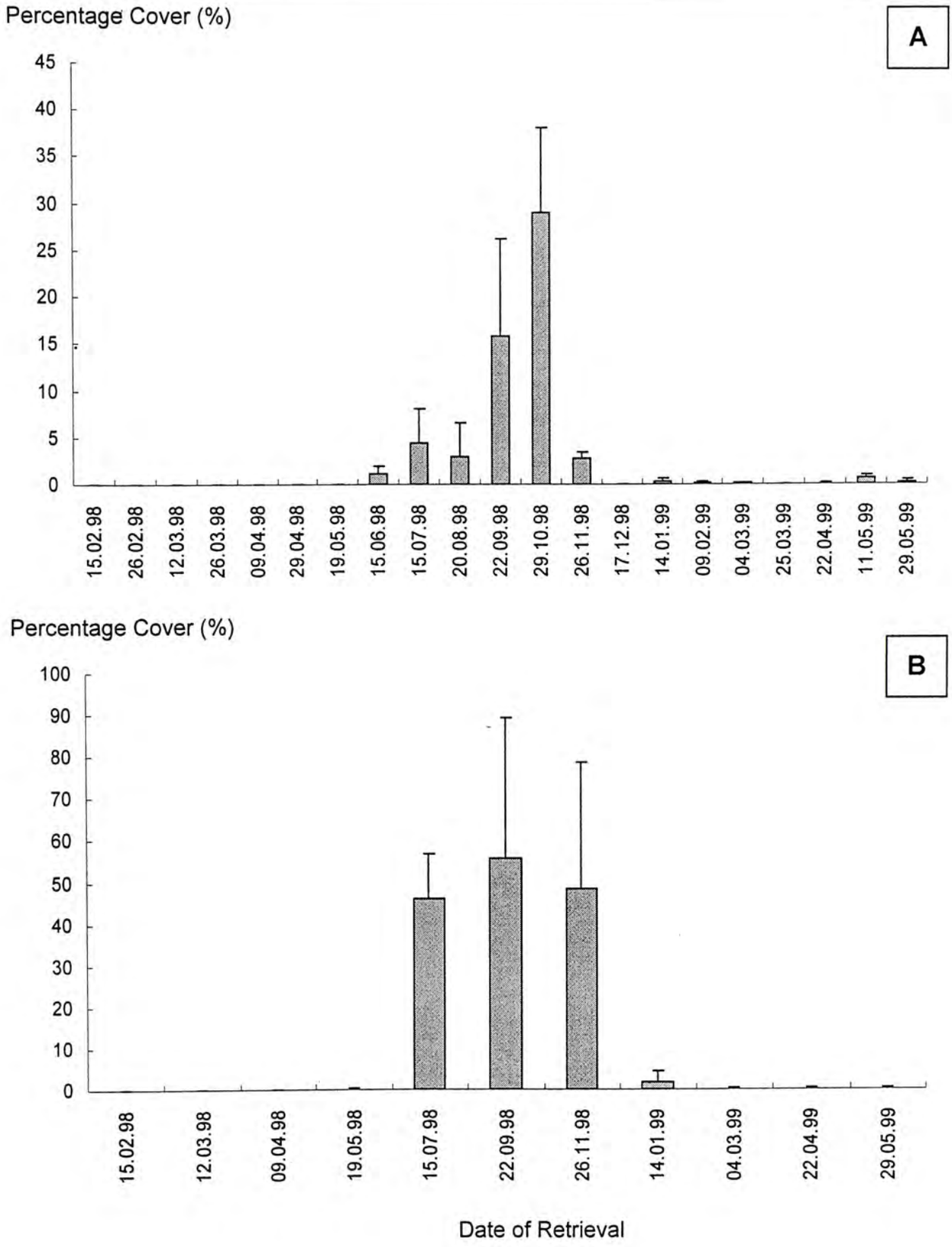


Fig. 4.8. Encrusting coralline algae. Changes in percentage cover (%, + SD, n = 4; n = 3 on 20-Aug 1998 for biweekly-retrieved tiles and on 29-May 1999 for monthly-retrieved tiles) on (A) biweekly- and (B) monthly-retrieved tiles in A Ma Wan from 15-Feb 1998 to 29-May 1999.

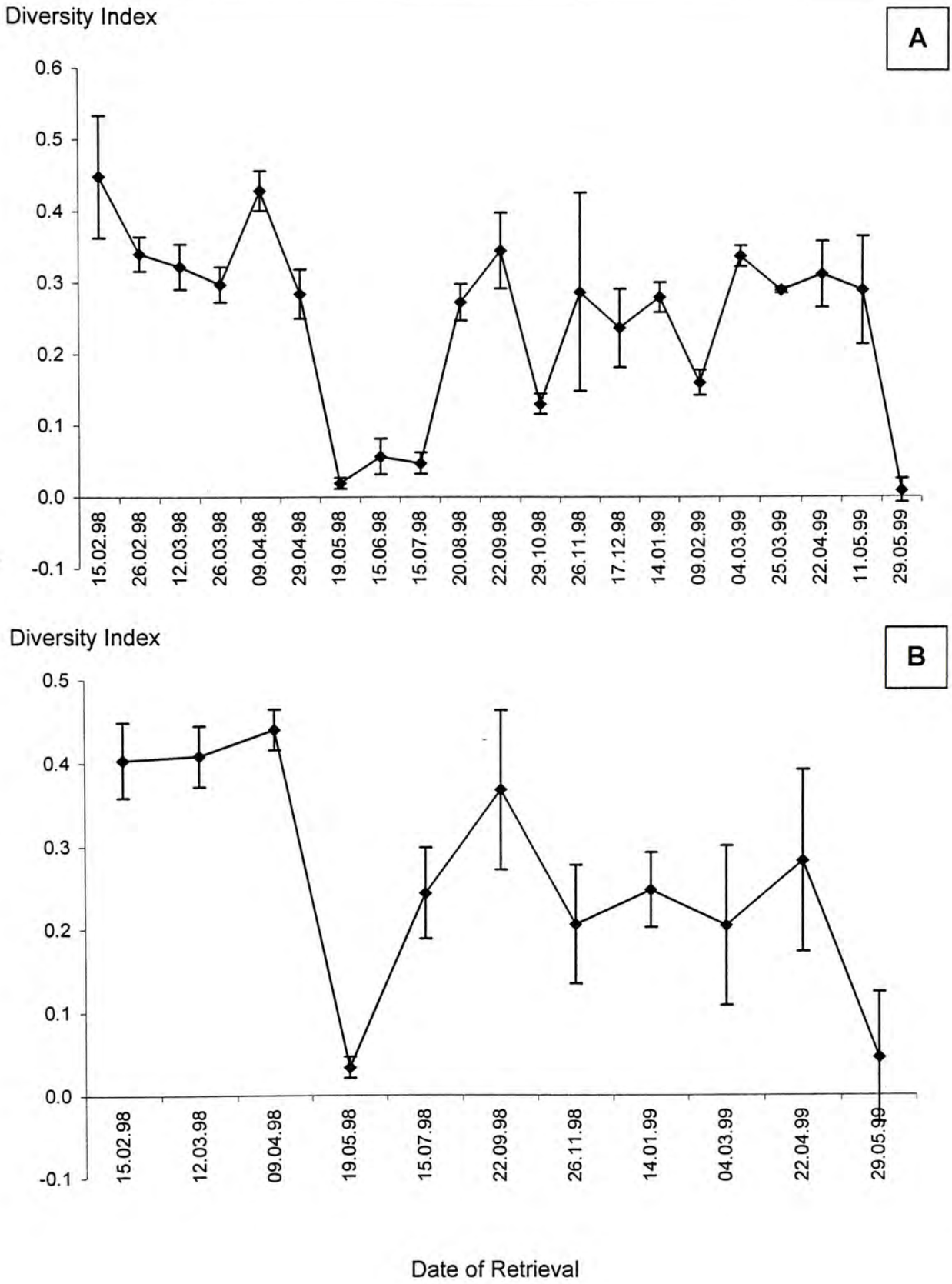


Fig. 4.9. Species diversity. Changes in Brillouin's species diversity index (± SD, n = 4; n = 3 on 20-Aug 1998 for biweekly-retrieved tiles and on 29-May 1999 for monthly-retrieved tiles) on (A) biweekly- and (B) monthly-retrieved tiles in A Ma Wan from 15-Feb 1998 to 29-May 1999.

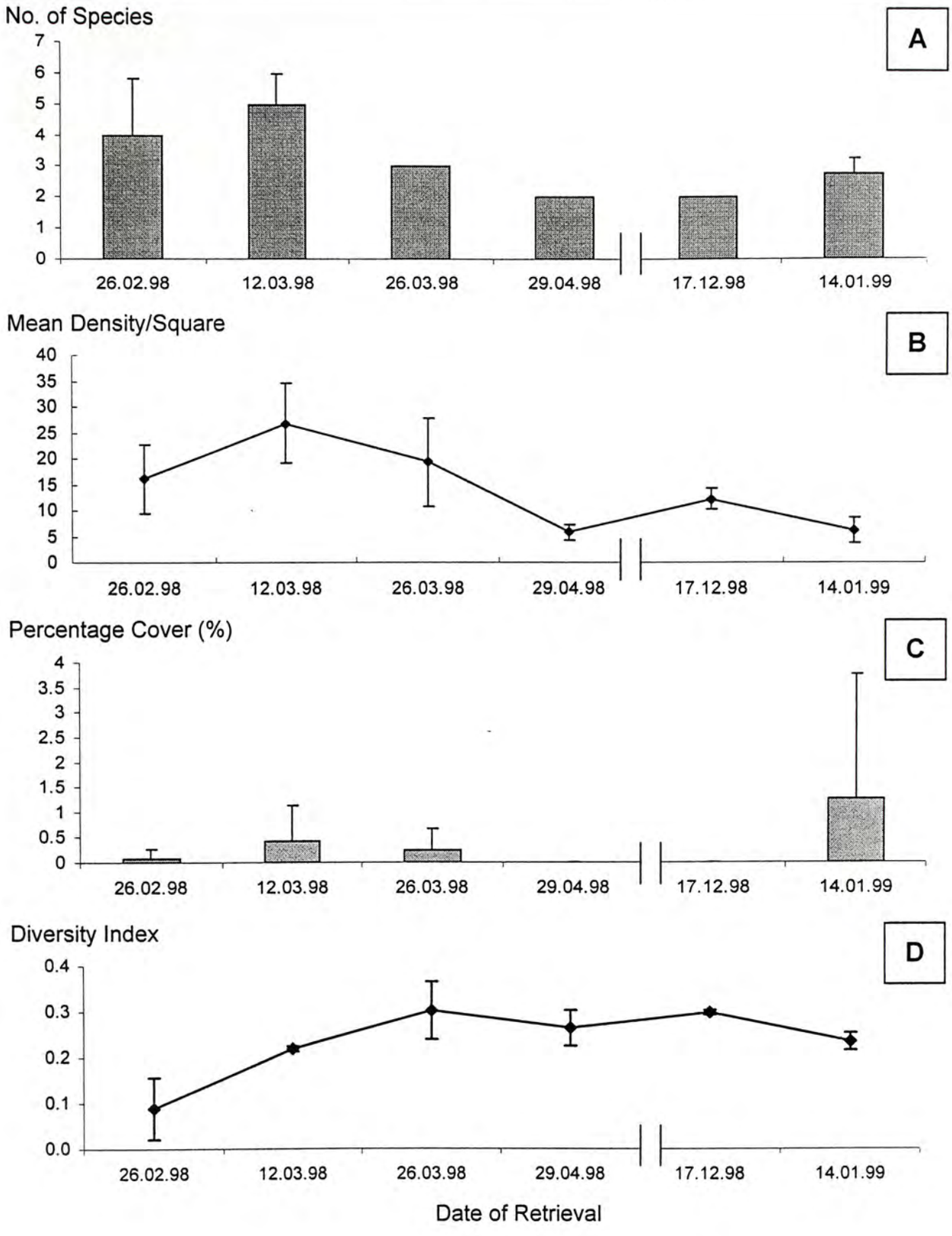


Fig. 4.10. Lung Lok Shui tiles at –2 to –3 m CD. Changes in (A) mean number of species (+ SD); (B) mean density (total number of individuals per 2 x 2 $mm^2$ square) (± SD); (C) percentage cover (%, + SD) of encrusting coralline algae, and (D) Brillouin's species diversity index on biweekly-retrieved tiles (n = 4; n = 3 on 12- & 26- Mar 1998) at –2 to –3 m CD in Lung Lok Shui from 26-Feb 1998 to 14-Jan 1999.

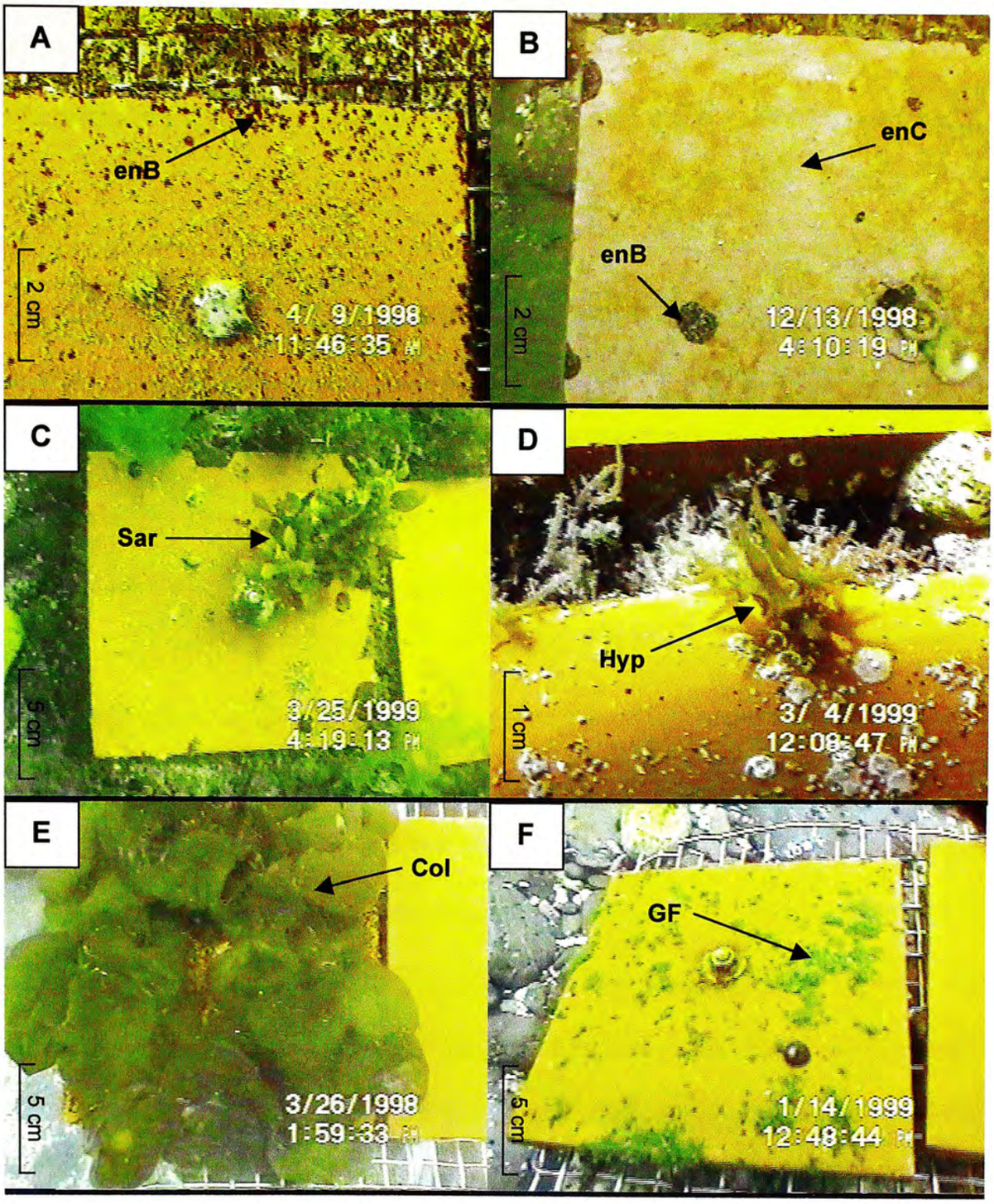


Fig. 4.11. Algal recruits recorded on permanently-placed tiles in A Ma Wan and Lung Lok Shui. (A) Encrusting brown algae (enB) appeared as tiny dots in A Ma Wan; (B) encrusting coralline algae (enC) and some large patches of encrusting brown algae in A Ma Wan; (C) a *Sargassum* (Sar) recruit observed in A Ma Wan; (D) a suspected *Hypnea* (Hyp) recruit on an extra tile in A Ma Wan; (E) a tile covered by recruits of *Colpomenia sinuosa* (Col) in Lung Lok Shui; (F) many clumps of filamentous green algae (GF) observed in Lung Lok Shui.

# Chapter 5

# Seasonal Availability of Algal Propagules at Different Water Depths

## 5.1 Introduction

In studies of algal colonization on cleared patches of natural substrata or introduced artificial substrata, temporal and spatial variations in recruitment patterns, species composition, richness, diversity and density, are usually observed. What is crucial to these variations in a community may not only be the types of propagules present but also the seasonal availability and viability of these propagules.

Most marine algae release their propagules after reproduction and disperse them in the forms of gametes, spores, zygotes, germlings and drifting plant parts like broken branches or fragments. They settle on open spaces and germinate into young sporelings under favourable environmental conditions. To a certain extent, all recruitment studies are related to an evaluation of the presence and absence of algal propagules. Equivalent to the idea of "seed rain" in land plants (Harper 1977), there is also "spore rain" for marine algae (see reviews by Hoffmann 1987 & Santelices 1990). Although the existence of algal propagules in water column is a common aspect of algal biology that has a fundamental importance in the formation of algal vegetation structure, it has received little attention by phycologists.

When studying the algal propagules in seawater, researchers paid much attention to the availability of these propagules in surface and/or running-off waters (Hruby & Norton 1979, Hoffmann & Ugarte 1985, Zechman & Mathieson 1985). Amsler & Searles (1980) documented the differences in the vertical distribution of algal spores in a water column off the North Carolina coast. They hypothesized that (1) some algae produce

spores which may spend long periods of time drifting around the middle or upper parts of a water column and hence, they have relatively large dispersal shadows; (2) other algae, instead, produce spores which mostly remain close to the bottom and thus, have small dispersal shadows. Amsler & Searles (1980) found that all the spores collected in the upper and middle parts of the water column were fugitive species while spores of Phaeophyta and Florideophyceae were more restricted to the bottom of the water column. Apart from the dispersal capabilities, Hoffmann & Ugarte (1985) believed that the composition of propagules in the seawater could also be determined by the species locally present as well as the reproductive patterns and periodicities of the taxa present on the shore (see also Reed *et al.* 1988).

Seasonal and spatial collection of water samples may allow a general pattern of the availability and viability of algal propagules from populations of the marine algae to be assessed. Thus, the purpose of the present experiment is to investigate the availability of algal propagules in seawater by seasonal collection of bottom water samples from three different water depths, −1 m CD, −2 to −3 m CD and −10 m CD, and also to examine the presence of propagules in the water column near the algal beds in both A Ma Wan and Lung Lok Shui. The resultant pattern may be correlated with changes in the physical conditions of seawater (e.g. pH, salinity, temperature). This information can also supplement the previous two recruitment studies by artificial clearings on natural rock surface in A Ma Wan (see Chapter 3) and the setting up of artificial substrata in both A Ma Wan and Lung Lok Shui (see Chapter 4).

## 5.2 Materials and Methods

### 5.2.1 Study sites and sample collection

Three water samples, about 4 to 5 L each, were collected in summer-fall (9-Sep 1998

to 11-Oct 1998), fall-winter (25-Nov 1998 to 8-Jan 1999), winter-spring (26-Jan 1999 to 15-Mar 1999) and spring-summer (1-Apr 1999 to 11-May 1999), at three different sites in both A Ma Wan and Lung Lok Shui. These four periods generally represented the four seasons, fall, winter, spring and summer respectively. The collection sites in A Ma Wan included the bottom areas at −1 m CD, near the population of *Hypnea charoides* (see Chapter 2) and the experimental set-ups of the ceramic tiles (see Chapter 4), at −2 to −3 m CD, where the attached individuals of *H. charoides* (on live or dead corals at −2 to −3 m CD) were collected (see Chapter 2), and at a depth of −10 m CD. Although in A Ma Wan, marine algae are seldom observed at −10 m CD, it is still possible that algal propagules are present in the water column. Besides, the collection of seawater there allows the comparison in the availability of algal propagules at the same depth between different sites. Similarly in Lung Lok Shui, samples were collected from the bottom water at −1 m CD and −2 to −3 m CD, both near the experimental set-ups of the ceramic tiles (see Chapter 4) and the former also near the population of *H. charoides* in which measurement of plant length and collection of samples for examining reproductive structures were carried out (see Chapter 2). Water samples were also collected a depth of −10 m CD, where a very well-grown population of *H. charoides* was found. The selections of these study sites allow the study of availability of algal propagules near the populations of marine algae (more particulary *H. charoides*) in both A Ma Wan and Lung Lok Shui. The information obtained can provide some insights for the previous studies on reproductive seasonality of *H. charoides* (see Chapter 2) and algal recruitment in Ping Chau (see Chapters 3 & 4).

Water samples at depths of −1 m CD and −2 to −3 m CD were collected by snorkeling while those from the depth of −10 m CD were collected by a reversing water sampler.

Physical parameters like pH, salinity and temperature of seawater were measured at the time of each sample collection.

### 5.2.2 Experimental design

After collection, water samples were taken back to the laboratory within two hours. Each water sample was poured into an aquarium (19 x 11 x 11.5 $cm^3$ in size). A total of 18 aquaria was set up each time. A piece of rectangular ceramic tile with an area of about 7.6 x 15.2 $cm^2$ was horizontally placed at the bottom of each aquarium for settlement of algal spores (Fig. 5.1A). These aquaria, each representing one replicate of the three water samples from different sites, were randomly placed on an iron rack (Fig. 5.1B) with their positions determined by a lottery draw. This rack was set up in an open but sheltered area, allowing the algal spores to have sufficient sunlight for growth. Continuous aeration was provided to each aquarium. The original seawater was replaced with artificial seawater (Instant Ocean) one week after collection. On a weekly basis thereafter, the artificial seawater was replaced to replenish the nutrients. An extra three aquaria with tiles at the bottom were set up during each settlement period and filled with artificial seawater as a control experiment. The artificial seawater inside these aquaria was also replaced at each time of replenishment.

Observation was done approximately one month after settlement. Two quadrats, each 5 x 5 $cm^2$ in size, with 200 random squares (same as the one used in the study of recruitment on ceramic tiles in Chapter 4) was used to examine the tiles, following the same methodology described earlier in the study of algal recruitment on artificial substrata (see Chapter 4). The recruited tiles were fully immersed in artificial seawater during examination and they were all examined within a period of one week.

5.2.3 Examination of tiles and statistical analyses

The algal recruits recorded on the rectangular tiles were investigated for their species composition, richness and diversity (Brillouin's index) following the methods described in Chapter 4. For frequency analysis, the number of squares in which a given species appeared over the total number of squares counted in a quadrat (i.e. 200 squares) was calculated and expressed in percentage.

Two Way ANOVA was applied to test if there were significant differences in species richness, percentage frequency and species diversity among different sites (–1 m CD, –2 to –3 m CD and –10 m CD water) and different seasons (fall, winter, spring and summer) in both A Ma Wan and Lung Lok Shui. Data were first tested for normality and homogeneity of variance using Kolmogorov-Smirnor and Levene Median tests respectively. Where the assumptions of normality and homogeneity could not be met, the data were transformed. Non-parametric tests were employed when all data transformations failed to meet the parametric assumptions. Data collected at different survey sites in different seasons were also compared in terms of species richness, percentage frequency and species diversity between A Ma Wan and Lung Lok Shui using Mann-Whitney Rank Sum Test. Correlation between these three variables and different physical parameters (pH, salinity and temperature of seawater) at different sites were also evaluated using Pearson Product Moment Correlation.

## 5.3 Results

5.3.1 Species composition

Algal recruits on the ceramic tiles in this study were all of very small sizes (< 1 mm in general). They were soft and easily destroyed by the sharp end of the probe when they were picked out for mounting, making species identification difficult. Therefore, the

algal recruits were identified and grouped according to their morphologies, similar to the way it was done in the previous recruitment study (see Chapter 4). A list of algal recruits, which were recorded in the water samples collected at depths of –1 m CD, –2 to –3 m CD and –10 m CD in both A Ma Wan and Lung Lok Shui from September 1998 to May 1999, is presented in Table 5.1. Each group was named and abbreviated according to its appearance and descriptions. Some of the species appeared to be the same as those observed in Chapter 4, such as filamentous brown (BF), brown patches (BP), encrusting coralline algae (C), filamentous green (GF), green patches (GP), filamentous red (RP), red patches (RP) and *Sphacelaria* propagules (Sph) (see Chapter 4 Table 4.1). Among all the species recorded, only *Sphacelaria* could be identified with certainty due to the production of its remarkable, often triradiate, asexual propagules. For the others, they could at best be described and classified by their pigmentation (brown/green/red) and other physical features (e.g. blades, filaments, clumps, stoloniferous, branching, thin, thick, fleshy, etc.).

### 5.3.2 Availability of algal propagules in A Ma Wan

#### 5.3.2.1 Species richness

In A Ma Wan, the mean number of species for–1 m CD samples was generally higher than that recorded at –2 to –3 m CD and –10 m CD in all seasons (Fig. 5.2A). It decreased slightly from 3.7 ± 2.4 in fall to 3.0 ± 0.6 in spring and increased to 4.2 ± 1.5 in summer. On the contrary, the number of species recorded in –2 to –3 m CD samples were the lowest in four seasons, ranging from 2.3 ± 0.8 in fall and 2.3 ± 0.5 in winter to 3.3 ± 1.0 in summer. In general, the trends for both –2 to –3 m CD and –10 m CD water samples were similar, in which the mean number of species increased gradually from fall to summer.

Since the data failed to meet the parametric assumptions after several attempts of transformation, Kruskal-Wallis One Way ANOVA on Ranks was applied respectively to test the differences of changes in species richness between different survey sites in the same season and between different seasons at the same site. Statistical results showed that there were neither significant differences ($p > 0.05$) found between different survey sites nor between different seasons.

5.3.2.2 Frequency

In water samples collected at −1 m CD, the mean percentage frequency decreased slightly from fall (31.7 ± 35.0 %) to winter (29.6 ± 17.0 %) and rose to its highest point (71.3 ± 11.0 %) in spring (Fig. 5.2B). It then dropped to the lowest point (21.7 ± 7.6 %) in summer. The mean frequency at −2 to −3 m CD increased gradually from its minimum (20.8 ± 18.8 %) in fall to the maximum (57.0 ± 10.0 %) in spring and decreased to 38.4 ± 16.0 % in summer. For samples collected from the depth of −10 m CD, the mean frequency did not rise but dropped gradually from 22.5 ± 14.0 % in fall to the minimum of 6.8 ± 4.4 % in spring. It then rose to its highest value (30.8 ± 17.0 %) in summer.

Statistical results showed that significant differences ($p < 0.05$) were found in changes of percentage frequency among different survey sites and seasons (Table 5.2, see also Appendix C Table C1.1) and there was a statistically significant interaction ($p < 0.05$) between sites and seasons.

Table 5.3 showed the mean percentage frequencies of different algal species in samples collected from the three survey sites in A Ma Wan in different seasons. Most species had very low frequencies, with values mostly less than 1 % (some were even

less than 0.1 %). They were present only in certain seasons in different sites. The dots (D), however, could be found in all seasons in all the sites at relatively high frequencies, ranging from 4.6 ± 3.9 % (summer) to 28.8 ± 32.8 % (fall) at –1 m CD, 2.9 ± 1.6 % (summer) to 33.5 ± 24.5 % (winter) at –2 to –3 m CD and 1.2 ± 0.6 % (summer) to 20.7 ± 14.7 % (fall) at –10 m CD. The green patches (GP) were also frequently observed (absent only in fall at –1 m CD and winter at –2 to –3 m CD), with relatively high frequencies in –10 m CD water samples. Another green, the filamentous green (GF), was mostly found in winter and summer, with especially high percentage frequencies in summer (14.4 ± 9.1 % at –1 m CD; 33.5 ± 17.0 % at –2 to –3 m CD; 12.3 ± 5.2 % at –10 m CD), while the branching filamentous green (bGF) was mainly observed in spring and its frequencies in –1 m CD (46.3 ± 14.9 %) and –2 to –3 m CD (37.4 ± 12.9 %) water samples were the highest amongst all the values recorded.

5.3.2.3 Species diversity

The species diversities (Fig. 5.2C) for the three survey sites generally increased from their minima (0.1 ± 0.1 at –1 m CD and –2 to –3 m CD; 0.2 ± 0.1 at –10 m CD) in fall to the maxima (0.3 ± 0.1 at –1 m CD and –2 to –3 m CD) in spring, except for –10 m CD samples, where the highest index (0.3 ± 0.0) was found in summer. The mean values recorded in deep water were relatively low in all seasons, except in spring, when the –10 m CD water samples showed the lowest frequency (0.2 ± 0.1).

Significant difference ($p < 0.05$) in changes in species diversity was only observed among different seasons but not between survey sites (Table 5.2, see also Appendix C Table C1.2), nor was there a significant interaction ($p > 0.05$) between sites and seasons.

5.3.3 Availability of algal propagules in Lung Lok Shui

5.3.3.1 Species richness

The mean numbers of species found in the three survey sites in Lung Lok Shui peaked in different seasons (Fig. 5.3A). At –1 m CD, the maximum was observed in fall (4.7 ± 0.5) while the minimum was in winter (2.5 ± 1.1). At –2 to –3 m CD, the highest value was recorded in winter (4.2 ± 1.5) while the lowest was in summer (2.0 ± 1.1). For –10 m CD samples, the number of species was the highest (4.0 ± 0.9) in spring but the lowest (2.0 ± 0.6) in winter.

Statistical results showed that there were neither significant differences ($p > 0.05$) found in changes of species richness among different survey sites nor among different seasons (Table 5.4). However, there was a significant interaction ($p < 0.05$) observed between sites and seasons.

5.3.3.2 Frequency

The patterns of changes in mean percentage frequencies appeared to be similar for the three survey sites (Fig. 5.3B), where they all dropped gradually from their maxima (39.3 ± 20.2 % at –1 m CD; 50.3 ± 50.6 % at –2 to –3 m CD; 33.1 ± 8.6 % at –10 m CD) in fall to their minima (10.3 ± 9.1 % at –1 m CD; 3.9 ± 1.9 % at –2 to –3 m CD; 5.3 ± 3.7 % at –10 m CD) in summer.

Significant difference ($p < 0.05$) in changes of percentage frequency was only observed among different seasons but not between survey sites (Table 5.4, see also Appendix C Table C2.1), nor was there a significant interaction ($P > 0.05$) between sites and seasons.

Changes in mean percentage frequencies of different algal species at –1 m CD, –2 to –3 m CD and –10 m CD in Lung Lok Shui (Table 5.5) were similar to those observed in A Ma Wan (Table 5.3). Most of the algal species showed very low frequencies (less than 1 % or even 0.1 %) and were only found in certain seasons. Likewise, the dots (D) was observed in all seasons for all the survey sites, with mean frequencies ranged from 3.2 ± 1.4 % (summer) to 33.9 ± 21.0 % (fall) at –1 m CD, 2.5 ± 1.0 % (summer) to 29.3 ± 18.6 % (fall) at –2 to –3 m CD and 1.3 ± 0.7 % (spring) to 29.5 ± 8.5 % (fall) at –10 m CD. However, unlike in A Ma Wan, the filamentous green (GF) and the green patches (GP) were found in all seasons for all the survey sites, but with relatively low values than those of the dots (D). The mean frequencies of the former ranged from 0.3 ± 0.4 % (winter) to 2.7 ± 2.8 % (summer) at –1 m CD, 0.8 ± 0.7 % (spring) to 8.3 ± 13.4 % (fall) at –2 to –3 m CD and 0.2 ± 0.3 % (winter) to 1.9 ± 4.7 % (fall) at –10 m CD while that of the latter ranged from 0.1 ± 0.2 % (fall and winter) to 3.7 ± 4.6 % (summer) at –1 m CD, 0.1 ± 0.2 % (fall) to 3.8 ± 3.7 % (winter) at –2 to –3 m CD and 0.2 ± 2.3 % (fall) to 5.7 ± 7.1 % (spring) at –10 m CD. The brown filamentous (BF) was another species which showed relatively high frequencies, particularly in the fall (3.2 ± 2.5 % at –1 m CD; 12.3 ± 20.0 % at –2 to –3 m CD).

5.3.3.3 Species diversity

Similar trends of changes in species diversity were observed at depths of –1 m CD and –10 m CD (Fig. 5.3C), in which the mean values decreased from fall to the lowest values (0.1 ± 0.1 at –1 m CD and –10 m CD) in winter and then gradually rose to their maxima in summer (0.3 ± 0.2) and spring (0.3 ± 0.1) respectively. In contrast, the mean diversity index of –2 to –3 m CD samples did not drop but increased gradually from fall to the highest (0.3 ± 0.1) in spring and then decreased to its minimum (0.1 ± 0.1) in summer.

Similar to changes in percentage frequency, significant difference ($p < 0.05$) in changes of species diversity was only observed among different seasons but not between survey sites (Table 5.4, see also Appendix C Table C2.2). There was also no significant interaction ($p > 0.05$) found between sites and seasons.

### 5.3.4 Comparisons between A Ma Wan and Lung Lok Shui

Statistical results indicated that data of species richness, percentage frequency and species diversity obtained at different survey sites in different seasons between A Ma Wan and Lung Lok Shui were mostly not significantly different ($p > 0.05$) (Table 5.6). Significant differences ($p < 0.05$) were only found at –2 to –3 m CD in winter in terms of species richness, at –1 m CD and –2 to –3 m CD in spring as well as at –2 to –3 m CD and –10 m CD in summer in terms of percentage frequency.

### 5.3.5 Physical parameters

Physical parameters like pH, salinity and temperature of seawater were recorded at the time when the water samples were collected on sites. In A Ma Wan, the patterns of changes in pH, salinity and seawater temperature were very similar to each other among the three survey sites (Fig. 5.4). For pH (Fig. 5.4A), they all gradually increased from the lowest (7.8 ± 0.0 at –1 m CD and –2 to –3 m CD; 7.8 ± 0.1 at –10 m CD) in fall to the highest (8.7 ± 0.1 at –1 m CD; 8.6 ± 0.0 at –2 to –3 m CD and –10 m CD) in summer. Such a large range in pH values was likely due to some experimental errors during measurement on site. Salinity did not fluctuate substantially with the minimum recorded as 29.0 ± 1.0 ‰ at –2 to –3 m CD in fall and the maximum recorded as 35.0 ± 0.0 ‰ at –10 m CD in summer (Fig. 5.4B). Seawater temperature was not recorded in the fall for all the three sites (Fig. 5.4C). Relatively low values were found in spring (20.3 ± 0.6 °C at –1 m CD; 20.7 ± 0.3 °C at –2 to –3 m CD; 18.0

± 0.0 °C at –10 m CD) and high values were observed in summer (23.5 ± 0.0 °C at –1 m CD; 23.3 ± 0.3 °C at –2 to –3 m CD; 23.3 ± 0.1 °C at –10 m CD).

Similar to A Ma Wan, the mean values of all the parameters recorded in Lung Lok Shui were very close to each other among the three survey sites (Fig. 5.5). The pH values gradually increased from the lowest in fall (7.8 ± 0.0 at –1 m CD; 7.9 ± 0.0 at –2 to –3 m CD; 7.8 ± 0.0 at –10 m CD) to the highest in summer (8.7 ± 0.0 at –1 m CD and –2 to –3 m CD; 8.6 ± 0.0 at –10 m CD) (Fig. 5.5A). This large range, similar to that recorded in A Ma Wan, might be due to some experimental errors during measurement. Whereas for salinity (Fig. 5.5B), the minimum value was recorded as 29.7 ± 0.6 ‰ at –1 m CD and –2 to –3 m CD in fall while the maximum value was 35.0 ± 0.0 ‰ at –10 m CD in summer among all the values recorded. For seawater temperature (Fig. 5.5C), the patterns appeared similarly to those observed in A Ma Wan in which relatively low values were recorded in spring (18.5 ± 0.0 °C at –1 m CD and –2 to –3 m CD; 18.3 ± 0.6 °C at –10 m CD) and high values were recorded in summer (23.5 ± 0.5 °C at –1 m CD; 23.3 ± 0.3 °C at –2 to –3 m CD; 23.4 ± 0.2 °C at –10 m CD). No data were recorded in fall.

### 5.3.6 Correlation

In A Ma Wan, changes in species richness, mean percentage frequency and species diversity were not significantly correlated to any changes in the physical parameters (pH, salinity and temperature of seawater) (Table 5.7). In Lung Lok Shui, however, negative correlations were observed between the mean percentage frequency and pH at –1 m CD ($r = -0.978$, $n = 4$, $p < 0.05$) and –2 to –3 m CD ($r = -0.982$, $n = 4$, $p < 0.05$). Furthermore, the mean percentage frequency was also negatively correlated to

changes in salinity in –1 m CD ($r = -0.954$, $n = 4$, $p < 0.05$) and –10 m CD ($r = -0.959$, $n = 4$, $P < 0.05$) water samples.

### 5.3.7 Other recruits

Apart from algae, there were a few tubeworms recruited from the water samples collected in A Ma Wan and Lung Lok Shui. They were all about 1 cm in length when observed and were mainly found in fall. Relatively more were recruited at –1 m CD (maximum up to 6 in A Ma Wan) but none was observed in –10 m CD water samples at both sites.

## 5.4 Discussion

Among the 15 algal species recorded, 8 were observed on the ceramic tiles in the previous recruitment study (Table 5.1, see Chapter 4 Table 4.1). As noted before, the dominant algal species recruited onto the tiles were the filamentous green (GF) and the green patches (GP) (see Chapter 4 Table 4.4). In this part of the research, however, the most abundant species were the dots (D) while these greens were the second dominant taxa (Tables 5.3 & 5.5). This indicates that the composition of these planktonic propagules obtained from culturing the water samples was a bit different from the recruited algal taxa obtained *in situ*, more particularly in A Ma Wan. Similar phenomenon was also observed in other places like the Firth of Clyde in Scotland (Hruby & Norton 1979) and New Hampshire in USA (Zechman & Mathieson 1985), where they found that the cultured water samples were dominated by green algae whereas the *in situ* populations were dominated by red and brown algae. Zechman & Mathieson (1985) then suggested a variety of interacting factors to address such kind of discrepancy, such as the varying reproductive strategies exhibited by *in situ* populations, including the motility of their propagules, and possibly, some phototactic

responses, shedding rhythms, discharge patterns (i.e. numbers), settling rates of individual or multiple propagules, and propagule longevity. Therefore, in order to determine the most striking factor(s) leading to the differences between the cultured and the *in situ* populations in Ping Chau, more information concerning the aspects suggested above is still needed.

The occurrence of the dots (D) was most consistent among all the species recorded throughout the whole study period. Changes in their percentage frequency showed a pronounced seasonality in all the water samples collected in A Ma Wan and Lung Lok Shui, indicating that a relatively high abundance of its propagules was found in fall and winter in both sites (Tables 5.3 & 5.5). During this investigation, the number of propagules of the dots (D) was highly variable between replicates simultaneously collected from the same site or even between quadrats of the same replicate. This could be explained by aggregated dispersal of propagules, which could contribute to a high variability in the quantity of algal spores between samples (Hoffmann & Ugarte 1985, Muñoz & Santelices 1994, see also Okuda & Neushul 1981). The filamentous green (GF), branching filamentous green (bGF) and green patches (GP) also showed marked seasonalities in A Ma Wan (Table 5.3). Such seasonalities, however, were not as obvious in Lung Lok Shui (Table 5.5), suggesting that there might be a spatial variation shown in the seasonal occurrence of algal species in Ping Chau. For the other species, they all appeared with much lower percentage frequencies (< 1 %). This indicates different viabilities exhibited by different algal species, in which some of them are more viable under changing conditions in their marine habitats and/or are more opportunistic in occupying a new space (see also Chapters 3 & 4).

In the previous recruitment study, algal recruits were observed on the ceramic tiles in

A Ma Wan throughout the whole year (see Chapter 4). It was suggested that algal spores or propagules were able to exist in some microscopic floating forms in the water column under adverse environmental conditions and recruit only when the conditions became favourable (e.g. winter). The results of the present experiment seem to agree with this in which algal spores were successfully collected from all the water samples of both A Ma Wan and Lung Lok Shui in the four seasons, implying that algal spores or propagules did exist in the water column in Ping Chau all year round. Significant differences found between seasons in terms of percentage frequency and species diversity in A Ma Wan and Lung Lok Shui suggested that there were temporal variations in the availability of algal spores in the water column. Such variations were much more obvious in changes in percentage frequency. In A Ma Wan, relatively high frequencies of algal recruitment were recorded at –1 m CD and –2 to –3 m CD in spring, indicating a greater amount of algal spores available during that period of time (Fig. 5.2B). This was further supported by the relatively high species diversities recorded at –1 m CD and –2 to –3 m CD (Fig. 5.2C). This may be so as spring was the growing season of many marine algae in A Ma Wan (see Chapters 2 & 3). This increased the number of fertile plants and hence, spore production and release. Marked difference was also observed in percentage frequency of recruits between different depths in A Ma Wan, suggesting that a greater number of algal spores could be obtained in shallower water areas (–1 to –3 m CD). This may be attributed to the distribution of marine algae in A Ma Wan, where most species grow abundantly within a depth zone of –1 to –3 m CD. This, therefore, increased the availability of algal spores in shallow water.

High temporal variations in the abundance of algal spores in seawater were evidently observed in the past in other places (Hruby & Norton 1979, Hoffman & Ugarte 1985,

Zechman & Mathieson 1985). Moreover, Hoffmann & Ugarte (1985) found that the abundance of propagules could vary according to the local algal composition. In the present study, the greatest abundance of algal spores was found during the peak growing and/or reproductive season of many marine algae in A Ma Wan, suggesting that the presence of local algal vegetation could influence the number of spores/propagules in the water column. This, in turn, suggests a relationship between the availability of algal spores and the reproductive seasonality of marine algae in A Ma Wan. On the contrary, the mean density of algal recruits recorded on the ceramic tiles was relatively low (generally lower than 15 ind. per square) at this period of high spore abundance (see Chapter 4 Fig. 4.7A). This is in contrast to the result obtained by Hruby & Norton (1979), who found that algal recruitment on frosted slides was positively correlated with spore abundance in seawater. Furthermore, Zechman & Mathieson (1985) showed that the highest number of propagules occurred just prior to the period of maximum biomass of marine algae on the shore. The present results thus indicate a certain degree of mortality exhibited by the algal spores in their actual environment.

In contrast to A Ma Wan, changes in percentage frequency observed in Lung Lok Shui showed relatively high values in the fall for the three groups of water samples (Fig. 5.3B). Although there was a deep algal population at the depth of −10 m CD (see Chapter 2), significant differences were not found between water samples collected from different depths with respect to all the variables investigated. This suggests that factors other than the presence of local algal vegetation affect the availability of algal spores in the water column in Lung Lok Shui. One of the possible reasons may be the wave action. Water motion affects marine algae in various ways. It may be a major cause of algal mortality at all stages of growth, more particularly for settling spores or

zygotes (Lobban & Harrison 1994, Azanza-Corrales *et al.* 1996). Nonetheless, strong water motion can facilitate algal dispersal (Reed *et al.* 1988). Moreover, turbulence can keep spores (re)suspended in the water column for further transport (Reed *et al.* 1988, Azanza-Corrales *et al.* 1996). The present study suggests that currents and waves together generate turbulence of seawater in Lung Lok Shui, leading to a mixing up of algal spores and thus, contributing to the similarity in trends observed in percentage frequency of propagules for the three groups of water samples. This can also explain the fact that seasonalities in percentage frequency of different algal species between depths were not as obvious as those observed in A Ma Wan. Despite this, however, temporal variations were still clearly shown in Lung Lok Shui.

Changes in species richness, percentage frequency and species diversity were generally not significantly correlated to any changes in the physical parameters (pH, salinity and temperature of seawater), more particularly in A Ma Wan (Table 5.7). In spite of this, significant negative correlations were observed in changes in percentage frequency with pH and/or salinity at –1 m CD and –2 to –3 m CD in Lung Lok Shui. Nevertheless, there were no correlations between these variables and seawater temperature. This is similar to the result obtained by Pacheco-Ruiz *et al.* (1989) but in contrast to other studies which showed that temporal variations in spore production was attributed to temperature fluctuations (Oza & Krishnamurthy 1968, Guzmán del Proo *et al.* 1972, see also Zechman & Mathieson 1985). While some workers observed that reduced salinity was important in causing propagule discharge (West 1972), the present results suggest a possibility that decrease in pH and/or salinity may increase the abundance of algal spores in Lung Lok Shui. This, however, requires a more detailed study to verify in the future.

This experiment indicates the existence of temporal and spatial variations in the availability of algal propagules between A Ma Wan and Lung Lok Shui. Furthermore, the reasons contributing to such variations may be different from site to site. A certain degree of mortality is suggested. This can affect the availability of algal propagules in the water column when compared with the *in situ* algal recruitment. Nonetheless, more information is still required in order to better understand all the phenomena observed as well as the influences of the surrounding environment on the dynamics of algal recruitment.

Table 5.1. Abbreviations of different algal groups recruited from water samples collected at different depths (–1 m CD, –2 to –3 m CD and –10 m CD) in both A Ma Wan and Lung Lok Shui and their descriptions. Species marked with "#" were recorded in the previous recruitment experiment (see Chapter 4).

| Algal groups | Descriptions |
|---|---|
| BB | Brown, appeared in blades |
| #BF | Brown, filamentous, appeared singly |
| cBF | Brown, filamentous, appeared in cluster |
| #BP | Brown, appeared in patches |
| #C | Encrusting coralline algae |
| D | Dots |
| #GF | Green, filamentous, appeared singly |
| bGF | Green, filaments, branching |
| #GP | Green, appeared in patches |
| #RF | Red, filamentous, appeared singly |
| bRF | Red, filamentous, branching |
| sRF | Red, filamentous, stoloniferous |
| tRF | Red, filamentous, thick and fleshy |
| #RP | Red, appeared in patches |
| Sph | Suspected *Sphacelaria* |

Table 5.2. Results of Two-Way ANOVA on changes in percentage frequency and species diversity among different survey sites (–1 m CD, –2 to –3 m CD and –10 m CD) and seasons (fall, winter, spring and summer) in A Ma Wan. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Variable | Source of Variance | DF | SS | MS | F | P |
|---|---|---|---|---|---|---|
| Frequency | Survey site | 2 | 5808.10 | 2904.10 | 9.5700 | 0.0002* |
| | Season | 3 | 4268.10 | 1422.70 | 4.6900 | 0.0052* |
| | Survey site x Season | 6 | 10374.1 | 1729.00 | 5.7000 | <0.0001* |
| | Residual | 60 | 18199.0 | 303.300 | | |
| | Total | 71 | 38649.3 | 544.400 | | |
| Species diversity | Survey site | 2 | 0.04970 | 0.02483 | 2.8170 | 0.0677 |
| | Season | 3 | 0.32080 | 0.10693 | 12.132 | <0.0001* |
| | Survey site x Season | 6 | 0.04500 | 0.00750 | 0.8510 | 0.5362 |
| | Residual | 60 | 0.52890 | 0.00881 | | |
| | Total | 71 | 0.94430 | 0.01330 | | |

Table 5.3. Mean percentage frequencies (% ± SD) of different algal groups in samples collected at –1 m CD, –2 to –3 m CD and –10 m CD in A Ma Wan in different seasons from September 1998 to May 1999 (n = 6). Values above or equal to 1 % are in bold.

| Algal groups | –1 m CD | | | | –2 to –3 m CD | | | | –10 m CD | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer |
| **BB** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **BF** | 0.3 ± 0.6 | 0.2 ± 0.4 | 0 | 0.1 ± 0.2 | 0.1 ± 0.2 | 0 | 0 | 0.1 ± 0.2 | 0.2 ± 0.3 | 0 | 0 | 0.1 ± 0.2 |
| **cBF** | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 |
| **BP** | 0.2 ± 0.4 | 0 | 0 | 0.4 ± 0.6 | 0 | 0 | 0 | 0.4 ± 1.0 | 0 | 0 | 0 | 0.4 ± 0.5 |
| **C** | 0.3 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **D** | **28.8 ± 32.8** | **25.3 ± 17.3** | **22.5 ± 5.6** | **4.6 ± 3.9** | **19.3 ± 17.5** | **33.5 ± 24.5** | **19.3 ± 6.1** | **2.9 ± 1.6** | **20.7 ± 14.7** | **14.5 ± 7.3** | **3.7 ± 3.9** | **1.2 ± 0.6** |
| **GF** | 0.8 ± 1.2 | **2.6 ± 1.8** | 0 | **14.4 ± 9.1** | 0 | **3.4 ± 1.3** | 0 | **33.5 ± 17.0** | 0 | 0.1 ± 0.2 | 0 | **12.3 ± 5.2** |
| **bGF** | 0.1 ± 0.2 | 0 | **46.3 ± 14.9** | 0 | 0 | 0 | **37.4 ± 12.9** | 0 | 0 | 0 | **1.8 ± 2.5** | 0 |
| **GP** | 0 | 0.7 ± 1.0 | **2.3 ± 3.1** | 0.9 ± 0.9 | 0.9 ± 1.5 | 0 | 0.3 ± 0.4 | **1.4 ± 1.0** | **1.2 ± 1.4** | **2.5 ± 1.9** | **1.1 ± 0.7** | **16.7 ± 13.0** |
| **RF** | 0.9 ± 0.6 | 0.3 ± 0.4 | 0.1 ± 0.2 | 0.9 ± 1.8 | 0.1 ± 0.3 | 0.3 ± 0.4 | 0 | 0 | 0 | 0.2 ± 0.3 | 0.1 ± 0.2 | 0 |
| **bRF** | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **sRF** | 0 | 0 | 0.1 ± 0.2 | 0.2 ± 0.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 |
| **tRF** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **RP** | 0.1± 0.2 | 0.1 ± 0.2 | 0 | 0.2 ± 0.3 | 0.3 ± 0.4 | 0 | 0 | 0.1 ± 0.2 | 0.5 ± 0.6 | 0.2 ± 0.4 | 0.2 ± 0.3 | 0.1 ± 0.2 |
| **Sph** | 0 | 0.5 ± 0.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 5.4. Results of Two-Way ANOVA on changes in species richness, percentage frequency and species diversity among different survey sites (–1 m CD, –2 to –3 m CD and –10 m CD) and seasons (fall, winter, spring and summer) in Lung Lok Shui. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Variable | Source of Variance | DF | SS | MS | F | P |
|---|---|---|---|---|---|---|
| Species richness | Survey site | 2 | 1.78000 | 0.88900 | 0.5310 | 0.5909 |
| | Season | 3 | 11.8200 | 3.94000 | 2.3520 | 0.0812 |
| | Survey site x Season | 6 | 30.8900 | 5.14800 | 3.0740 | 0.0109* |
| | Residual | 60 | 100.500 | 1.67500 | | |
| | Total | 71 | 144.990 | 2.04200 | | |
| Frequency | Survey site | 2 | 0.35000 | 0.17500 | 2.9700 | 0.0589 |
| | Season | 3 | 5.66500 | 1.88830 | 32.040 | <0.0001* |
| | Survey site x Season | 6 | 0.50000 | 0.08340 | 1.4200 | 0.2238 |
| | Residual | 60 | 3.53600 | 0.05890 | | |
| | Total | 71 | 10.0520 | 0.14160 | | |
| Species diversity | Survey site | 2 | 0.00625 | 0.00313 | 0.1680 | 0.8457 |
| | Season | 3 | 0.27857 | 0.09286 | 4.9910 | 0.0037* |
| | Survey site x Season | 6 | 0.17559 | 0.02926 | 1.5730 | 0.1708 |
| | Residual | 60 | 1.11627 | 0.01860 | | |
| | Total | 71 | 1.57668 | 0.02221 | | |

Table 5.5. Mean percentage frequencies (% ± SD) of different algal groups in samples collected at –1 m CD, –2 to –3 m CD and –10 m CD in Lung Lok Shui in different seasons from September 1998 to May 1999 (n = 6). Values above or equal to 1 % are in bold.

| Algal groups | –1 m CD | | | | –2 to –3 m CD | | | | –10 m CD | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer |
| **BB** | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **BF** | **3.2 ± 2.5** | 0 | 0.3 ± 0.6 | 0.5 ± 1.0 | **12.3 ± 20.0** | 0.1 ± 0.2 | 0.1 ± 0.2 | 0 | 0.8 ± 0.8 | 0 | 0.3 ± 0.4 | 0 |
| **cBF** | 0.1 ± 0.2 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 |
| **BP** | 0.1 ± 0.2 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0.2 ± 0.3 | 0 | 0 | 0 |
| **C** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **D** | **33.9 ± 21.0** | **18.3 ± 7.8** | **12.1 ± 15.7** | **3.2 ± 1.4** | **29.3 ± 18.6** | **22.1 ± 7.1** | **6.0 ± 3.1** | **2.5 ± 1.0** | **29.5 ± 8.5** | **9.9 ± 3.0** | **1.3 ± 0.7** | **1.8 ± 2.0** |
| **GF** | 0.5 ± 0.6 | 0.3 ± 0.4 | **1.0 ± 0.8** | **2.7 ± 2.8** | **8.3 ± 13.4** | **1.0 ± 1.0** | 0.8 ± 0.7 | **1.1 ± 1.4** | **1.9 ± 4.7** | 0.2 ± 0.3 | **1.3 ± 1.8** | 0.4 ± 0.4 |
| **bGF** | 0 | 0 | 0 | 0.3 ± 0.6 | 0 | 0 | 0.3 ± 0.5 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 |
| **GP** | 0.1 ± 0.2 | 0.1 ± 0.2 | **2.7 ± 3.4** | **3.7 ± 4.6** | 0.1 ± 0.2 | **3.8 ± 3.7** | **2.9 ± 2.6** | 0.3 ± 0.4 | 0.2 ± 2.3 | 0.6 ± 0.7 | **5.7 ± 7.1** | **2.7 ± 2.2** |
| **RF** | 0.9 ± 0.6 | 0 | 0 | 0 | 0.3 ± 0.4 | 0.4 ± 0.2 | 0 | 0.1 ± 0.2 | 0.1 ± 0.2 | 0.1 ± 0.2 | 0 | 0 |
| **bRF** | 0 | 0 | 0 | 0 | 0 | 0.1 ± 0.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| **sRF** | 0 | 0 | 0.7 ± 0.6 | 0 | 0 | 0 | 0.2 ± 0.3 | 0 | 0 | 0 | 0 | 0.3 ± 0.2 |
| **tRF** | 0 | 0 | 0 | 0 | 0 | 0.2 ± 0.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| **RP** | 0.5 ± 0.5 | 0 | 0.2 ± 0.4 | 0 | 0.1 ± 0.2 | 0 | 0.1 ± 0.2 | 0 | 0.5 ± 0.4 | 0 | 0.5 ± 0.4 | 0.3 ± 0.3 |
| **Sph** | 0 | 0.2 ± 0.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 5.6. Results of comparisons in species richness, percentage frequency and species diversity at the three survey sites (–1 m CD, –2 to –3 m CD and –10 m CD water) in different seasons (fall, winter, spring and summer) between A Ma Wan and Lung Lok Shui by Mann-Whitney Rank Sum Test. Significant difference (< 0.05) is indicated by an asterisk (*).

| | | Fall | Winter | Spring | Summer |
|---|---|---|---|---|---|
| –1 m CD | Species richness | 0.485 | 0.240 | 0.394 | 0.240 |
| | Percentage frequency | 0.485 | 0.180 | 0.002* | 0.240 |
| | Species diversity | 0.132 | 0.132 | 0.589 | 0.937 |
| –2 to –3 m CD | Species richness | 0.818 | 0.041* | 0.485 | 0.065 |
| | Percentage frequency | 0.240 | 0.937 | 0.002* | 0.002* |
| | Species diversity | 0.937 | 0.093 | 0.699 | 0.589 |
| –10 m CD | Species richness | 0.394 | 0.394 | 0.132 | 0.310 |
| | Percentage frequency | 0.394 | 0.180 | 0.589 | 0.004* |
| | Species diversity | 0.936 | 0.065 | 0.240 | 0.485 |

Table 5.7. Correlation of species richness, mean percentage frequency and species diversity with different physical parameters (pH, salinity and temperature of seawater) at different depths (–1 m CD, –2 to –3 m CD and –10 m CD) in A Ma Wan (AMW) and Lung Lok Shui (LLS). Each value represents the Pearson Product Moment Correlation coefficient "r" (n = 4). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| Site | | Variables | pH | Salinity | Temperature |
|---|---|---|---|---|---|
| AMW | –1 m CD | Species richness | 0.360 | 0.367 | -0.716 |
| | | Mean Frequency | -0.063 | -0.026 | 0.885 |
| | | Species diversity | 0.869 | 0.870 | 0.542 |
| | –2 to –3 m CD | Species richness | 0.841 | 0.849 | 0.899 |
| | | Mean Frequency | 0.633 | 0.620 | -0.692 |
| | | Species diversity | 0.752 | 0.742 | -0.416 |
| | –10 m CD | Species richness | 0.788 | 0.737 | 0.695 |
| | | Mean Frequency | 0.083 | 0.061 | 0.995 |
| | | Species diversity | 0.888 | 0.841 | 0.567 |
| LLS | –1 m CD | Species richness | -0.636 | -0.844 | -0.478 |
| | | Mean Frequency | -0.978* | -0.954* | -0.569 |
| | | Species diversity | 0.465 | 0.111 | -0.065 |
| | –2 to –3 m CD | Species richness | -0.265 | -0.079 | -0.529 |
| | | Mean Frequency | -0.982* | -0.910 | -0.080 |
| | | Species diversity | -0.115 | -0.090 | -0.942 |
| | –10 m CD | Species richness | 0.049 | -0.339 | -0.366 |
| | | Mean Frequency | -0.949 | -0.959* | -0.751 |
| | | Species diversity | 0.632 | 0.287 | -0.126 |

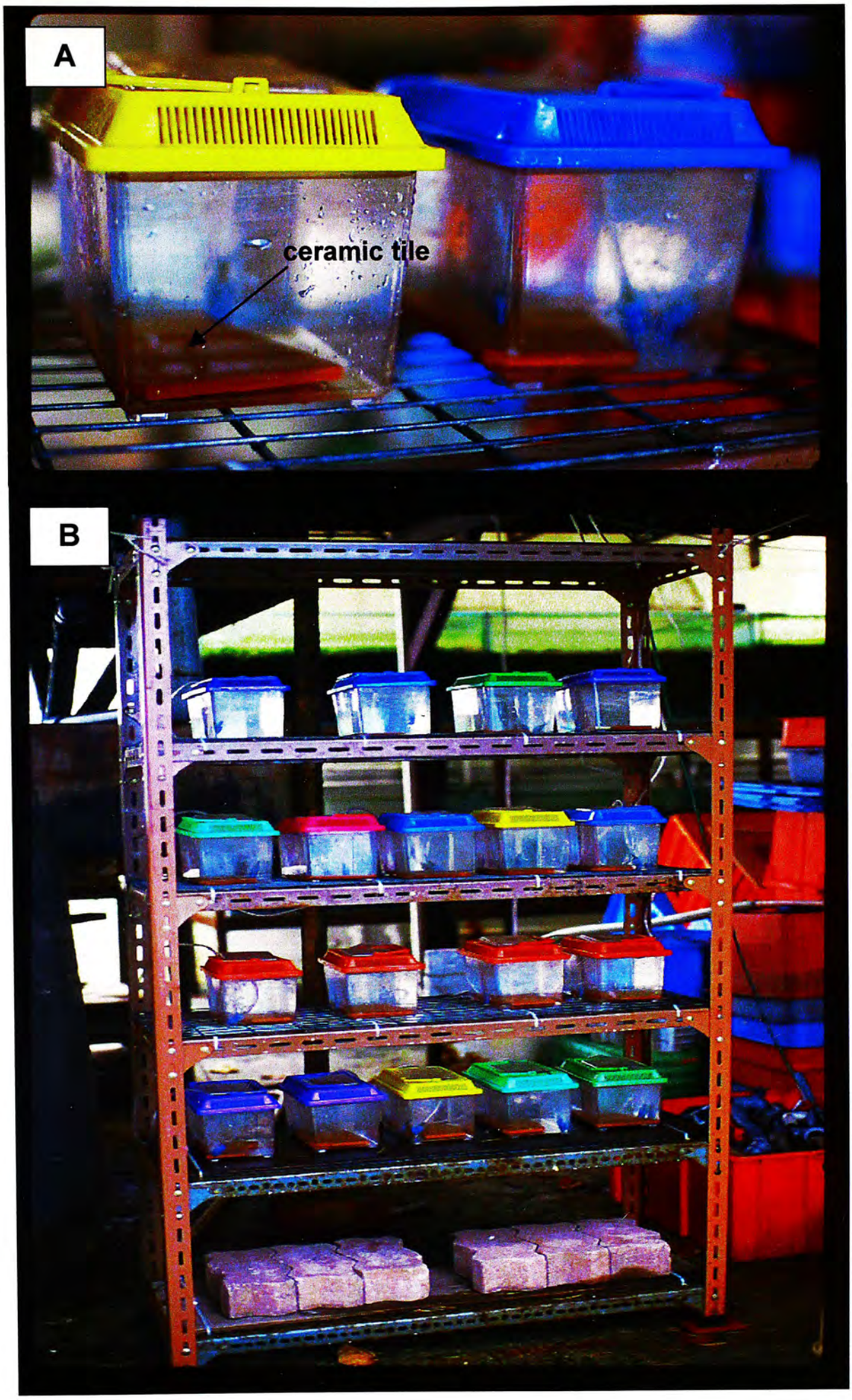


Fig. 5.1. Experimental set-up. (A) Aquaria with recruitment tiles; (B) 18 aquaria (water samples) randomly placed on the iron rack.

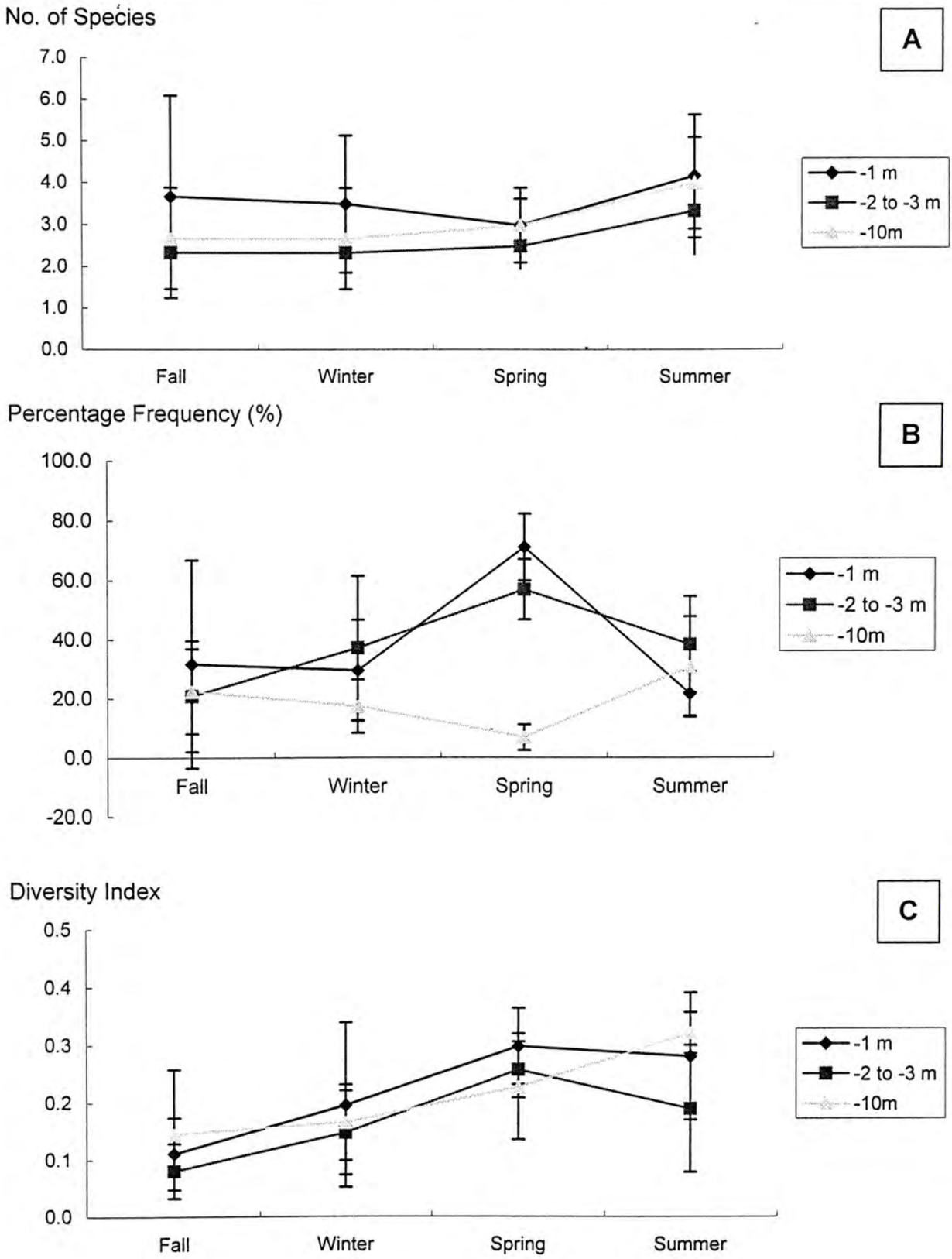


Fig. 5.2. A Ma Wan variables. Changes in (A) species richness, (B) percentage frequency (%) and (C) species diversity (± SD, n = 6) in samples collected at –1 m CD, –2 to –3 m CD and –10 m CD in A Ma Wan from fall 1998 to summer 1999.

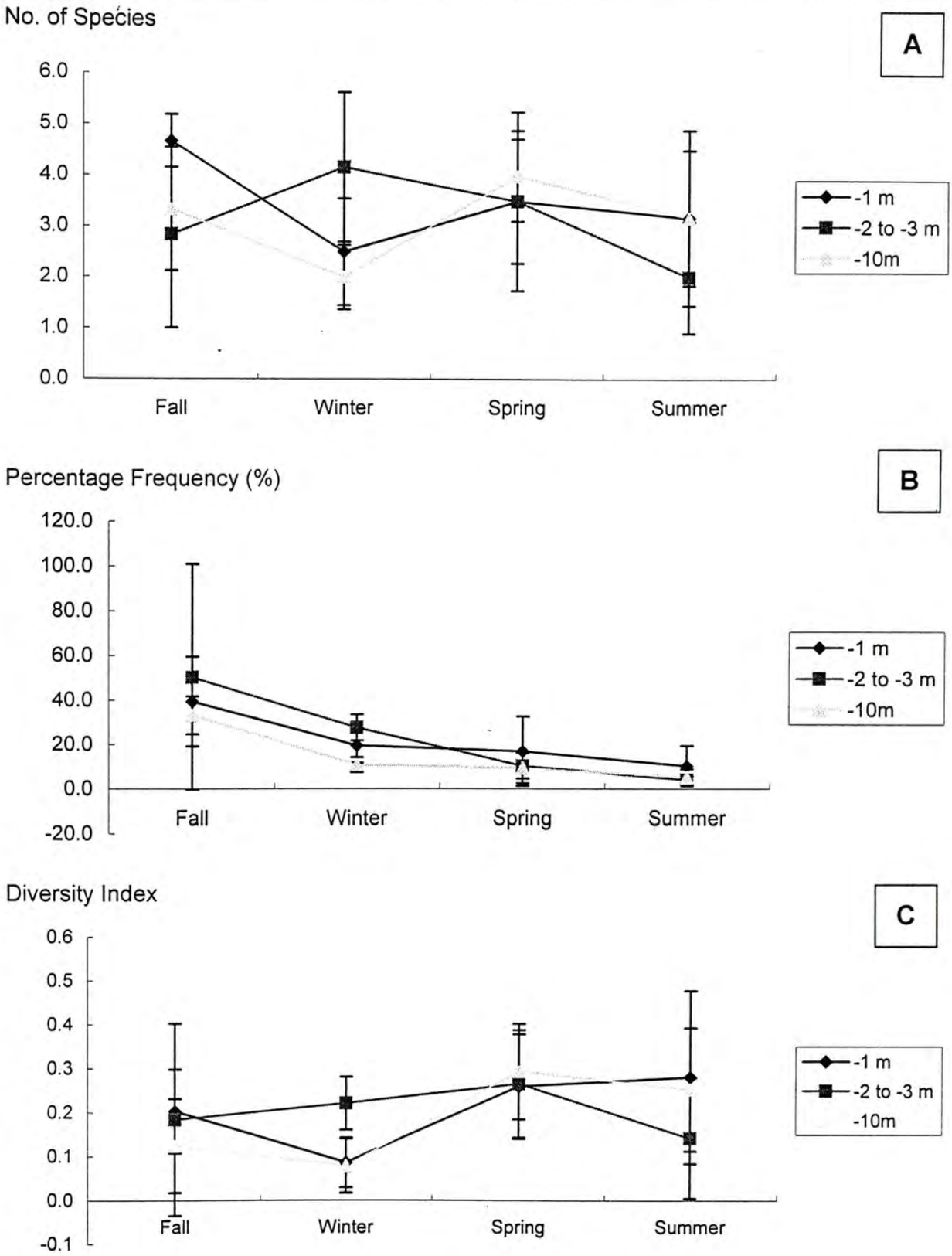


Fig. 5.3. Lung Lok Shui variables. Changes in (A) species richness, (B) percentage frequency (%) and (C) species diversity (± SD, n = 6) in samples collected at –1 m CD, –2 to –3 m CD and –10 m CD in Lung Lok Shui from fall 1998 to summer 1999.

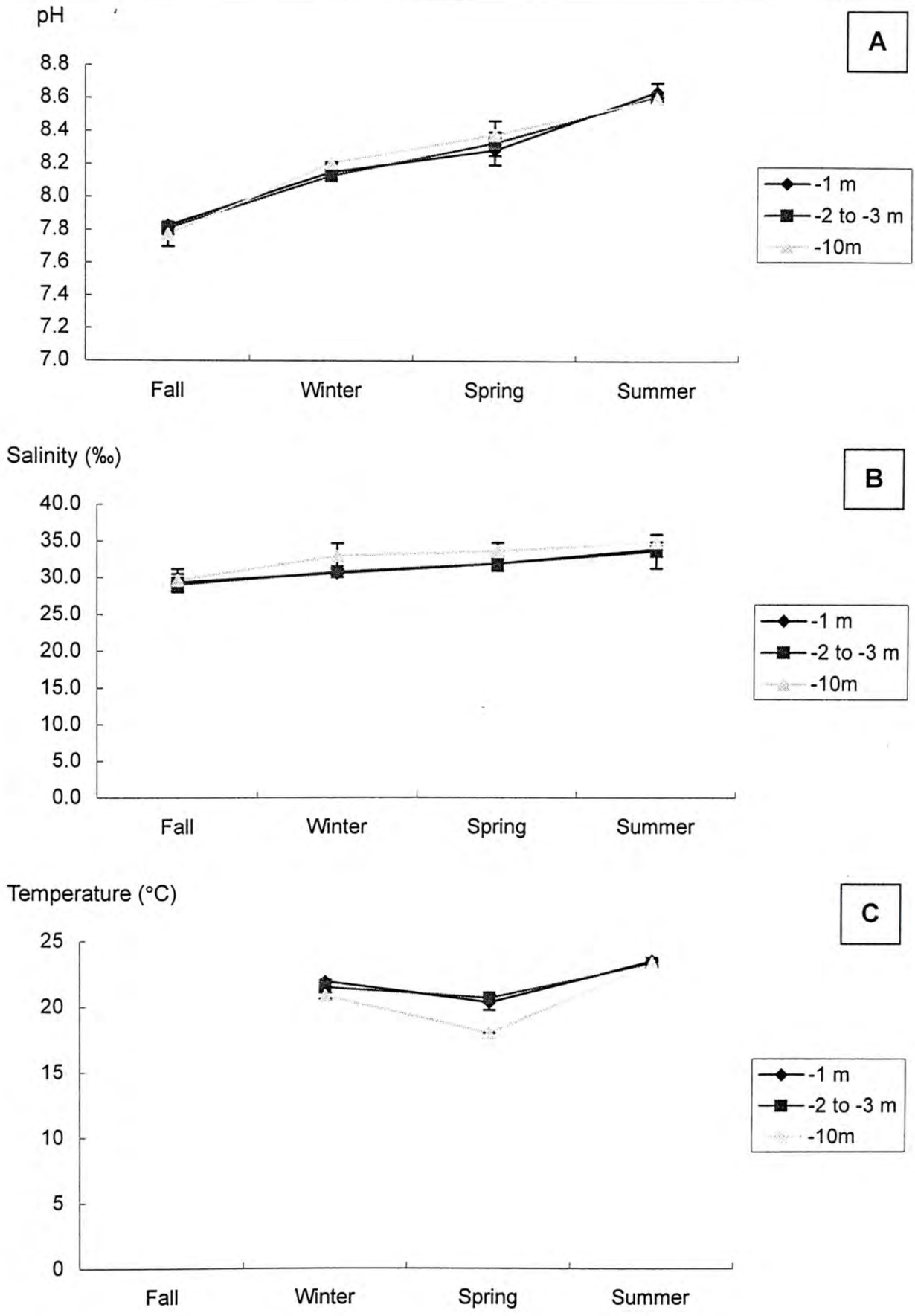


Fig. 5.4. A Ma Wan parameters. Changes in (A) pH, (B) salinity (‰) and (C) temperature (°C) (± SD, n = 3) in samples collected at –1 m CD, –2 to –3 m CD and –10 m CD in A Ma Wan from fall 1998 to summer 1999.

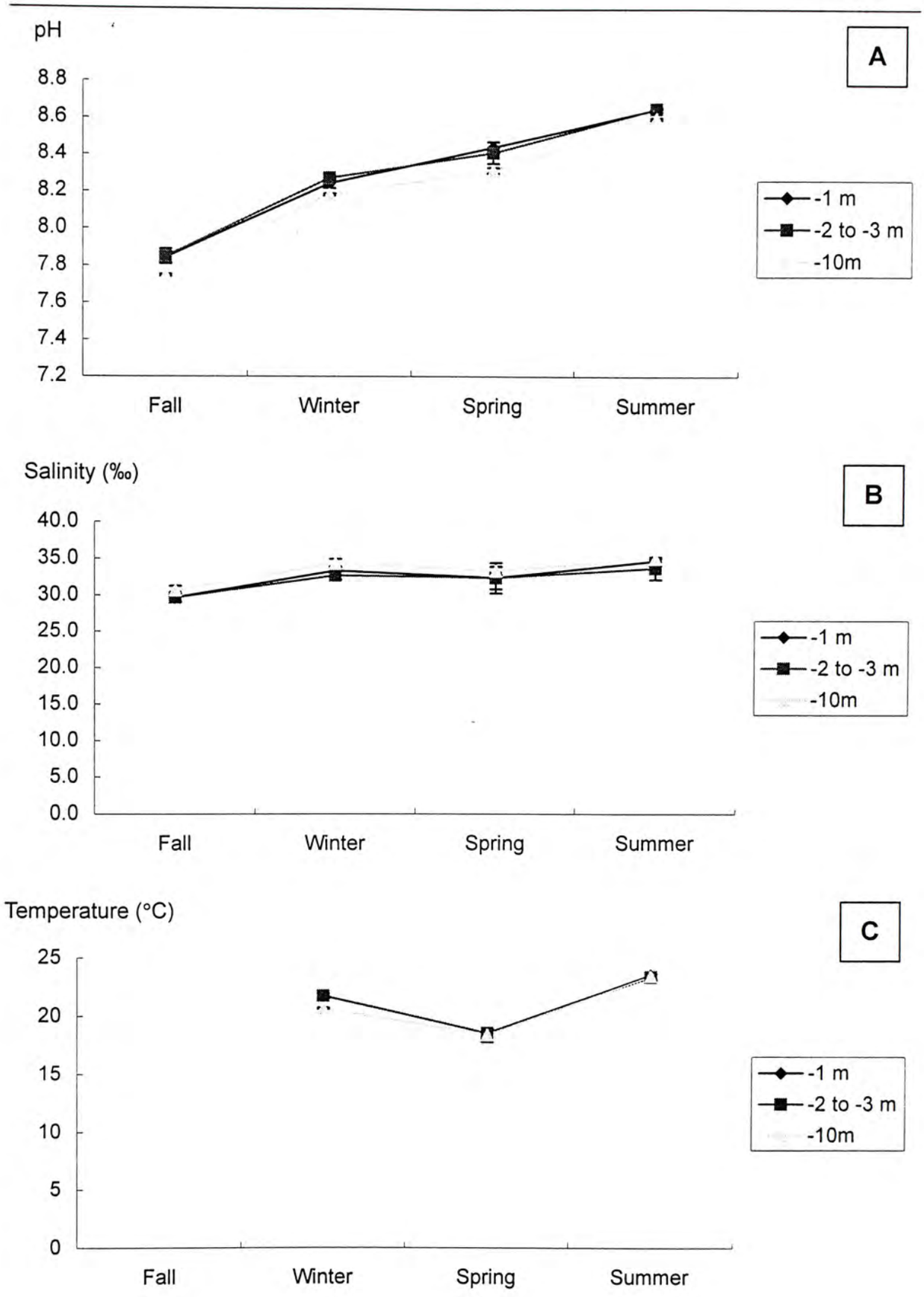


Fig. 5.5. Lung Lok Shui parameters. Changes in (A) pH, (B) salinity (‰) and (C) temperature (°C) (± SD, n = 3) in samples collected at –1 m CD, –2 to –3 m CD and –10 m CD in Lung Lok Shui from fall 1998 to summer 1999.

# Chapter 6

# General Discussion

Reproduction is one of the most important characteristics of all living organisms as they need to perpetuate their lives from generation to generation. For those which grow and/or reproduce seasonally, reproduction depends on having favourable conditions of the surrounding environment and hence, is much restricted to occur within a particular time. In Hong Kong, most marine algae are very seasonal in nature, showing abundant growth during winter and die-back during summer. As these marine plants play an important role in structuring the coastal communities, it is noteworthy to know when their growing and reproductive seasons start and end as well as the factors that affect the onset of these seasons.

In this research, seasonal occurrence and reproduction of the common red alga, *Hypnea charoides*, in Ping Chau were addressed (Chapter 2). It was observed that its populations in A Ma Wan and Lung Lok Shui generally occurred in winter and spring (November/December to April/May) but disappeared during summer and fall from 1996 to 1999. Annual growth of *H. charoides* was favoured by shorter photoperiod and lower seawater temperature, and the initiation of this growth was more likely induced by changes in seawater temperature rather than photoperiod in A Ma Wan. In contrast, none of these physical parameters was significantly correlated with the growth of the populations in Lung Lok Shui. Induction of growth by physical parameters (photoperiod and seawater temperature) was only observed in a population at the depth of −10 m CD. Both waves and currents are much stronger in Lung Lok Shui than in A Ma Wan. This may increase the fragmentation of the thalli of *H. charoides*, resulting in various sizes of individuals. Hence, the

influences of photoperiod, seawater temperature as well as nutrient concentrations on the seasonal growth pattern were much reduced.

Dominance of vegetative and tetrasporic plants and rarity of cystocarpic plants, which were reported in many other red algal species before, were observed in populations of *H. charoides* in both A Ma Wan and Lung Lok Shui (Chapter 2). Variations in physical parameters appear to be less important in triggering the onset of reproduction in these populations but significantly positive correlation was observed between the percentage occurrence of tetrasporic plants and seawater temperature, suggesting that increase in seawater temperature may enhance tetrasporogenesis in populations of *H. charoides*. It is possible that the lifespan of *H. charoides*, from fertilization of gametes to carposporophytes and from carpospores to the development of tetrasporophytes, is very short, leading to rare occurrence of cystocarpic plants. Besides, majority of the plants may undergo apomeiosis to complete their life cycles. Thus, populations of *H. charoides* in Ping Chau may first appear as infertile individuals, which can be gametophytes or tetrasporophytes, and become tetrasporic, releasing tetraspores at the end of the growing season. These tetraspores may be able to persist under adverse conditions (i.e. summer months with longer photoperiod and warmer temperature) in some microscopic floating forms and give rise to gametophytes that exhibit a very short fertilization process, or directly to tetrasporophytes by undergoing apomeiosis, to complete their life cycles in the next growing season.

The presence of an unusual growth period in Lung Lok Shui populations from July to November in 1998 indicates the ability of *H. charoides* to survive and grow during summer months (i.e. longer photoperiod and warmer temperature). During this

growth period, *H. charoides* obviously exhibited a heterotrichous organization, i.e. its thallus was differentiated into a prostrate form and an erect form. This appears to be a means of increasing opportunities to widely perennate its thallus throughout the whole area. Although the reason for the occurrence of this unusual growth period is not clear, it is possible that some endogenous regulations are involved.

A substratum for attachment is one of the important resource pools for sessile marine organisms. In Ping Chau (more so in Lung Lok Shui), *H. charoides* is mostly found drifting in the water column and entangled with other algal species, although a number of individual clumps can be found loosely attached on the rock surface. Setting up two types of experimental plots (chiselled vs hammered) on natural substrata in the clearing experiment (Chapter 3) provided open spaces for marine algae to settle and at the same time, helped distinguish whether the plants growing on the clearing plots developed from regeneration of the remnants embedded on the rock surface or from recruitment of newly settled algal propagules. Similar recruitment patterns shown in chiselled and hammered plots as well as in control plots indicate that marine algae in Ping Chau are most probably recruited from propagules, and not from regeneration of remnants from previous year's growth. However, whether they are recruited by spores, sporelings or fragments of the adult plants and where did these propagules come from remain unclear.

Pronounced annual variations were observed in the species composition and percentage cover of the algal recruits, implying that recruitment and growth patterns of marine algae in a specific place may vary significantly between years. Therefore, information obtained from a single growing season would not be enough to give any conclusive evidence on the recruitment pattern of marine algae in a given place.

Environmental conditions within marine habitats may change from year to year. Among the environmental parameters (photoperiod, seawater temperature and nutrient concentrations in seawater) investigated, relatively high seawater temperature in the winter of 1999, significant differences found in the concentrations of nitrites (much higher in 1998) and nitrates (much higher in 1999) in seawater between 1998 and 1999 may be some of the factors that led to this annual variation in algal recruitment patterns in Ping Chau. There is, however, some constancy amidst such variation. The recruitment patterns of the experimental plots cleared in 1998 appeared to be the same as those cleared in 1999 after the summer die-off, indicating that all variations in patterns of recruitment would finally terminate at the same point of stability after being exposed to some overly dominating external conditions: high temperature and daytime low tide in summer. Die-off during this time leveled off all the recruitment histories of these clearing plots.

The frequency of *H. charoides* occurring as independent thalli on the experimental plots and its percentage cover were both found to be relatively low among all the algal recruits recorded. This indicates that *H. charoides* did not appear to constitute a major part in the algal composition of the recruits on the experimental plots (including control, chiselled and hammered plots). Nevertheless, it is possible that *H. charoides* successfully occupied an open space by forming an algal complex with *Centroceras* spp. This algal complex is the most dominant "species" among all the recruits recorded throughout the study period. In addition to recruiting into the clearing plots, some encroachment of this complex from the periphery around the plots was also observed. This latter, although contributed only a minor part in the overall process of algal recruitment, is nevertheless a viable alternative mechanism to occupy an open space. Hence, one factor leading to the success of *H. charoides* to

retain its abundance in Ping Chau may be the ability for it to exist as a turf former. On the other hand, its ability to cling onto and get entangled with other algae, rather than being washed and carried away by waves, also helps to maintain its dominance. Therefore, vegetative propagation by broken branches appears to be an important mechanism for *H. charoides* to spread its population widely in Ping Chau during its growing season.

Recruitment of *H. charoides* in Ping Chau appears to be more successful in the growing season of 1998 than that of 1999. This is evidenced by the occurrence of *H. charoides* recruits on the clearing plots cleared in November 1997 to March 1998, in which they were mainly observed in April 1998 (i.e. they mostly appeared about one to three months after the plots were cleared) but were completely absent on the clearing plots created in or after November 1998. This implies that recruitment by spores or reproductive propagules occurred from December 1997 to April 1998, when the populations of *H. charoides* grew densely in A Ma Wan, and could carry on thereafter. Coincidence between spore recruitment and the period of increasing abundance of tetrasporophytes from March to April 1998 suggests that recruits of *H. charoides* could come from carpospores or even tetraspores. It is also possible that these spores released at the end of the growing season existed as some microscopic floating forms or persisted in the form of an algal complex during summer and developed its erect plant parts when environments allowed. The presence of *H. charoides* recruits in 1999 only in plots cleared in or before August 1998 further indicates that recruits of *H. charoides* could also come from regeneration of the remnants of preceding year or recruitment of vegetative branches from the population nearby. Therefore, recruitment by spores or reproductive propagules of *H. charoides* populations may happen within a very wide window throughout the

year. The existence of heterotrichy (i.e. short branches embedded in the algal complex) is beneficial to the widespreading of its population and is an effective mechanism to pre-empt the limited space even if recruitment from spores or propagules is unsuccessful.

The other two recruitment studies, setting up artificial substrata in sea bottom (Chapter 4) and in laboratory aquaria (Chapter 5), provided a general idea on the fate of the early assemblages of algae and the availability of algal spores in water column in Ping Chau respectively. Ceramic tiles were used as the artificial substrata in these two studies. The introduction of different recruitment tiles, i.e. biweekly-retrieved, monthly-retrieved and permanently-placed tiles, in the former experiment provided the opportunity to examine the recruitment patterns of micro- and macro-recruits. Significant differences in the patterns shown on biweekly- and monthly-retrieved tiles with respect to algal species composition, species richness, mean density, percentage cover of encrusting coralline algae and species diversity over time indicate significant temporal variations in these recruitment patterns. Although algal recruits were observed throughout the year, relatively high number of species was recorded from mid to late fall. Peak recruitment (i.e. highest density of algal recruits) was observed in summer and late fall on both types of tiles. These peaks coincided with the periods after the past growing season and before the start of the next one for most marine algae in A Ma Wan. Increase in the number of fertile plants at the end of the growing season increases the availability of propagules. These algal spores or propagules may not all settle on the rocky substratum immediately after they are released. Some may exist in microscopic floating forms in the water column during summer and fall. The continuous presence of algal recruits on the recruitment tiles throughout the study period indicates that settlement

of these propagules is going on throughout the year but they probably become successful only when conditions are favourable (i.e. late-fall to winter). Similar recruitment patterns shown on biweekly- and monthly-retrieved tiles and a few records of adult plants on the permanently-placed tiles indicate a high mortality rate of algal recruits during the recruitment process. Although only limited observations were available on recruitment tiles placed in Lung Lok Shui, a marked difference was observed in species composition between them and those placed in A Ma Wan. Some permanently-placed tiles in Lung Lok Shui were fully covered by recruits of *Colpomenia sinuosa* and many clumps of filamentous green algae but not in A Ma Wan during the same period of time, indicating the existence of spatial variations in algal recruitment patterns between the two study sites.

The availability of algal propagules in seawater was investigated by seasonal collection of bottom water samples from different water depths (–1 m CD, –2 m to –3 m CD and –10 m CD) and culturing the samples in aquaria (Chapter 5). The experimental results indicate that algal spores were available in all seasons in Ping Chau. Significant differences found between seasons in terms of percentage frequency and species diversity in A Ma Wan and Lung Lok Shui suggest that there are temporal and spatial variations in the availability of algal spores. A more pronounced difference was observed in A Ma Wan in terms of percentage frequency in which relatively high frequencies were recorded in –1 m CD and –2 to –3 m CD samples in spring, coinciding with the period of high number of fertile marine algae. Inconsistency in the composition of the planktonic propagules and recruitment peaks between the *in situ* and cultured ceramic tiles, more particularly in A Ma Wan, implies that differential degrees of mortality are probably exhibited by the algal spores in their actual environment.

Significant differences were not found between water samples collected from different depths with respect to all the variables investigated in Lung Lok Shui. The presence of strong waves, generating turbulence that mixes up the algal spores in the water column, probably contributes to the homogeneity in the percentage frequency of algal spores present in the water column.

It appears that the populations of *H. charoides* in Ping Chau exist mainly vegetatively. The increase in the percentage occurrence of tetrasporic plants at the end of the growing season helps produce large number of tetraspores, many of which may be able to survive under adverse conditions (e.g. summer) suspended in the water column. Population recruitment of *H. charoides* as well as that of many other algae is probably by spores or propagules, which are available in the water column throughout the year. Once recruited, *H. charoides* first appeared as an algal complex mixed with similarly heterotrichous *Centroceras* spp. such that they all can occupy a new space successfully. Erect individuals will only develop when conditions allow. Due to its ability or the ability of its broken branches to cling onto other algae, *H. charoides* can spread its populations successfully by vegetative fragmentation. Thus, asexual reproduction by fragmentation may also be one of the most important strategies for their perpetuation during the growth season.

There are temporal variations in the availability of algal propagules coupled with high mortality rates of the recruits during recruitment processes. Spatial variations in the recruitment patterns are also observed between sites. All these suggest that although a general pattern of algal growth and recruitment may be predictable between years, inter-annual variations at the micro-scale may be very stochastic and thus difficult to predict.

Whatever the past algal recruitment and growth pattern in a specific site may be, limitation imposed by the dominant physical environment, i.e. summer conditions, may wipe out all these recruitment histories. As a result, the success of a new growth season may thus largely depend on the availability of the propagules in the water column or the perennation of old remnants persisting as turfs to commence this new cycle. In effect, both sexual reproduction, by way of propagule production, and asexual reproduction, by way of vegetative growth from a prostrate base or vegetative fragmentation play critical roles in the population dynamics of *H. charoides* in Ping Chau.

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Table A1. Pairwise comparisons on species richness between different months of measurement (from February 1998 to June 1999) in control plots by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Feb-98 | Mar-98 | Apr-98 | May-98 | Jun-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Apr-99 | Jun-99 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Feb-98 | | – | – | – | – | * | – | * | – | – | – | * |
| Mar-98 | | | – | – | – | * | * | * | – | – | – | * |
| Apr-98 | | | | – | – | * | – | * | – | – | – | * |
| May-98 | | | | | – | – | – | – | – | – | – | * |
| Jun-98 | | | | | | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | – | – | – | – | – | – |
| Nov-98 | | | | | | | | – | – | – | – | – |
| Dec-98 | | | | | | | | | – | – | – | – |
| Jan-99 | | | | | | | | | | – | – | – |
| Feb-99 | | | | | | | | | | | – | – |
| Apr-99 | | | | | | | | | | | | – |
| Jun-99 | | | | | | | | | | | | |

Table A2.1. Pairwise comparisons on species richness between different months of measurement (from January 1998 to June 1999) and treatment plots (chiselled vs hammered) of Nov-97 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Jan-98 | | Feb-98 | | Mar-98 | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Jan-98 | C | | – | * | * | * | * | * | * | * | * | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | * | * | * | * | * | * | * | * | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Feb-98 | C | | | | * | – | – | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Mar-98 | C | | | | | | – | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Apr-98 | C | | | | | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| May-98 | C | | | | | | | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Jun-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Aug-98 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | | | – | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | | | | | | | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | | | | | – |

Table A2.2. Pairwise comparisons on species richness between different months of measurement (from February 1998 to June 1999) and treatment plots (chiselled vs hammered) of Jan-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Feb-98 | | Mar-98 | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Feb-98 | C | | – | * | * | * | * | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | * | * | * | * | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Mar-98 | C | | | | – | * | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Apr-98 | C | | | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| May-98 | C | | | | | | | | – | * | * | * | * | * | * | * | * | * | * | – | – | * | * | – | * | – | * |
| | H | | | | | | | | | * | * | * | * | – | – | * | – | * | * | – | – | – | – | – | – | – | – |
| Jun-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | * | – | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | – | * | – | – | – | – | – | – |
| Aug-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | * | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | | |

Table A2.3. Pairwise comparisons on species richness between different months of measurement (from March 1998 to June 1999) and treatment plots (chiselled vs hammered) of Feb-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Mar-98 | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Mar-98 | C | | – | * | * | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | * | * | – | – | * | * | * | * | * | * | * | * | * | * | * | * | – | * | – | – |
| Apr-98 | C | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| May-98 | C | | | | | | * | * | * | * | * | – | – | – | * | – | * | * | * | – | * | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Jun-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Aug-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | |

Table A2.4. Pairwise comparisons on species richness between different months of measurement (from April 1998 to June 1999) and treatment plots (chiselled vs hammered) of Mar-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Apr-98 | C | | – | – | – | * | * | – | * | – | – | – | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | – | – | * | * | * | * | * | * | * | * | – | – | – | * | * | – | * | * | * | * |
| May-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | * | * |
| Jun-98 | C | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Aug-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | * | * |
| Feb-99 | C | | | | | | | | | | | | | | | | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | * | * |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | |

Table A2.5. Pairwise comparisons on species richness between different months of measurement (from May 1998 to June 1999) and treatment plots (chiselled vs hammered) of Apr-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| May-98 | C | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Jun-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Aug-98 | C | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | | | * | – | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | |

Table A2.6. Pairwise comparisons on species richness between different months of measurement (from June 1998 to June 1999) and treatment plots (chiselled vs hammered) of May-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Jun-98 | C | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | – | – | – | – | – | – | * | – | – | – | – | – | – | – | | |
| Aug-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | – | – | – | – | * | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | – | – | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | * | * |
| Dec-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | * | * |
| Jan-99 | C | | | | | | | | | | – | – | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | – | – | – | – | – | – | * | * |
| Feb-99 | C | | | | | | | | | | | | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | | | – | – | – | – | * | * |
| Mar-99 | C | | | | | | | | | | | | | | – | – | – | * | * |
| | H | | | | | | | | | | | | | | | – | – | * | * |
| Apr-99 | C | | | | | | | | | | | | | | | | – | * | * |
| | H | | | | | | | | | | | | | | | | | * | * |
| Jun-99 | C | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | |

Table A2.7. Pairwise comparisons on species richness between different months of measurement (from November 1998 to June 1999) and treatment plots (chiselled vs hammered) of Aug-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Nov-98 | C | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | – | – | – | – | – | * | * |
| | H | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | – | * | * |
| | H | | | | | | | | | | | | | * | * |
| Jun-99 | C | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | |

Table A2.8. Pairwise comparisons on species richness between different months of measurement (from December 1998 to June 1999) and treatment plots (chiselled vs hammered) of Nov-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Dec-98 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H |
| Dec-98 | C | | – | * | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | – | – | – | – | – | * | – |
| | H | | | | | – | – | – | – | – | * |
| Mar-99 | C | | | | | | – | – | – | * | – |
| | H | | | | | | | – | – | – | * |
| Apr-99 | C | | | | | | | | – | * | – |
| | H | | | | | | | | | – | * |
| Jun-99 | C | | | | | | | | | | – |
| | H | | | | | | | | | | |

Table A2.9. Pairwise comparisons on species richness between different months of measurement (from February to June 1999) and treatment plots (chiselled vs hammered) of Dec-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H |
| Feb-99 | C | | – | – | – | – | – | * | * |
| | H | | | – | – | – | – | * | * |
| Mar-99 | C | | | | – | – | – | * | * |
| | H | | | | | – | – | * | * |
| Apr-99 | C | | | | | | – | * | * |
| | H | | | | | | | * | * |
| Jun-99 | C | | | | | | | | – |
| | H | | | | | | | | |

Table A2.10. Pairwise comparisons on species richness between different months of measurement (from February to June 1999) and treatment plots (chiselled vs hammered) of Jan-99 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H |
| Feb-99 | C | | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – |
| Mar-99 | C | | | | – | – | – | * | * |
| | H | | | | | – | – | * | * |
| Apr-99 | C | | | | | | – | – | – |
| | H | | | | | | | – | – |
| Jun-99 | C | | | | | | | | – |
| | H | | | | | | | | |

Table A2.11. Pairwise comparisons on species richness between different months of measurement (from April to June 1999) and treatment plots (chiselled vs hammered) of Mar-99 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|
| | | C | H | C | H |
| Apr-99 | C | | – | * | * |
| | H | | | * | – |
| Jun-99 | C | | | | – |
| | H | | | | |

Table A3.1. Pairwise comparisons on species richness between different clearing plots (Nov-97 and Jan-98) and control plots in the same month of measurement (February 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Control |
|---|---|---|---|
| Nov-97 | | * | – |
| Jan-98 | | | * |
| Control | | | |

Table A3.2. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98 and Feb-98) and control plots in the same month of measurement (March 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Control |
|---|---|---|---|---|
| Nov-97 | | * | – | – |
| Jan-98 | | | * | – |
| Feb-98 | | | | – |
| Control | | | | |

Table A3.3. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98 and Mar-98) and control plots in the same month of measurement (April 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Control |
|---|---|---|---|---|---|
| Nov-97 | | – | – | * | – |
| Jan-98 | | | – | – | – |
| Feb-98 | | | | * | – |
| Mar-98 | | | | | * |
| Control | | | | | |

Table A3.4. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98 and Apr-98) and control plots in the same month of measurement (May 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | Control |
|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | * | – |
| Jan-98 | | | – | – | * | – |
| Feb-98 | | | | – | – | – |
| Mar-98 | | | | | – | – |
| Apr-98 | | | | | | – |
| Control | | | | | | |

Table A3.5. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98 and May-98) and control plots in the same month of measurement (June 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Control |
|---|---|---|---|---|---|---|---|
| Nov-97 | | * | * | * | * | – | – |
| Jan-98 | | | – | – | – | – | – |
| Feb-98 | | | | – | – | – | – |
| Mar-98 | | | | | – | – | – |
| Apr-98 | | | | | | – | – |
| May-98 | | | | | | | – |
| Control | | | | | | | |

Table A3.6. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98 and Aug-98) and control plots in the same month of measurement (November 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Control |
|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | * | – |
| Mar-98 | | | | | – | – | * | – |
| Apr-98 | | | | | | – | – | – |
| May-98 | | | | | | | * | – |
| Aug-98 | | | | | | | | – |
| Control | | | | | | | | |

Table A3.7. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98 and Nov-98) and control plots in the same month of measurement (December 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Control |
|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | * | – | – | – |
| Jan-98 | | | – | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | – | – | – |
| Mar-98 | | | | | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – |
| May-98 | | | | | | | – | * | * |
| Aug-98 | | | | | | | | – | – |
| Nov-98 | | | | | | | | | – |
| Control | | | | | | | | | |

Table A3.8. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Mar-98, Apr-98 and May-98) and control plots in the same month of measurement (January 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Mar-98 | Apr-98 | May-98 | Control |
|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – |
| Jan-98 | | | – | – | – | * |
| Mar-98 | | | | – | – | – |
| Apr-98 | | | | | – | – |
| May-98 | | | | | | – |
| Control | | | | | | |

Table A3.9. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98, Nov-98, Dec-98 and Jan-99) and control plots in the same month of measurement (February 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | – | – | – | * | – |
| Feb-98 | | | | – | – | – | – | – | – | – | – |
| Mar-98 | | | | | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – |
| Dec-98 | | | | | | | | | | * | – |
| Jan-99 | | | | | | | | | | | – |
| Control | | | | | | | | | | | |

Table A3.10. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98, Nov-98, Dec-98, Jan-99, Feb-99 and Mar-99) and control plots in the same month of measurement (April 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Mar-99 | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | – | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | – | – | – | – | – | – | – |
| Mar-98 | | | | | – | – | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – | – | – |
| Dec-98 | | | | | | | | | | – | * | – | – |
| Jan-99 | | | | | | | | | | | – | – | – |
| Feb-99 | | | | | | | | | | | | – | * |
| Mar-99 | | | | | | | | | | | | | – |
| Control | | | | | | | | | | | | | |

Table A3.11. Pairwise comparisons on species richness between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98, Nov-98, Dec-98, Jan-99, Feb-99, Mar-99 and Apr-99) and control plots in the same month of measurement (June 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Mar-99 | Apr-99 | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | * | * | * | * | * | * | * | * | * | * | * |
| Jan-98 | | | – | * | * | * | * | * | * | * | * | * | * | * |
| Feb-98 | | | | * | * | * | * | * | * | * | * | * | * | * |
| Mar-98 | | | | | – | – | – | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – | – | – | – |
| Dec-98 | | | | | | | | | | – | – | – | – | – |
| Jan-99 | | | | | | | | | | | – | – | – | – |
| Feb-99 | | | | | | | | | | | | – | – | – |
| Mar-99 | | | | | | | | | | | | | – | – |
| Apr-99 | | | | | | | | | | | | | | – |
| Control | | | | | | | | | | | | | | |

Table A4. Pairwise comparisons on the first record of species richness between different clearing plots (pooled data) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Mar-99 | Apr-99 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – | – | – | – | * |
| Jan-98 | | | – | – | – | – | – | – | – | – | – | – | * |
| Feb-98 | | | | – | * | – | * | * | – | – | * | – | * |
| Mar-98 | | | | | – | – | – | – | – | – | – | – | * |
| Apr-98 | | | | | | – | – | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – | – | – |
| Dec-98 | | | | | | | | | | – | – | – | * |
| Jan-99 | | | | | | | | | | | – | – | – |
| Feb-99 | | | | | | | | | | | | – | – |
| Mar-99 | | | | | | | | | | | | | – |
| Apr-99 | | | | | | | | | | | | | |

Table A5. Pairwise comparisons on species diversity between different months of measurement (from February 1998 to June 1999) in control plots by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Feb-98 | Mar-98 | Apr-98 | May-98 | Jun-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Apr-99 | Jun-99 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Feb-98 | | – | – | – | – | * | * | * | – | – | – | * |
| Mar-98 | | | – | – | – | * | * | * | – | – | – | * |
| Apr-98 | | | | – | – | * | * | * | – | – | – | * |
| May-98 | | | | | – | – | – | – | – | – | – | – |
| Jun-98 | | | | | | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | – | – | – | – | – | – |
| Nov-98 | | | | | | | | – | – | – | – | – |
| Dec-98 | | | | | | | | | – | – | – | – |
| Jan-99 | | | | | | | | | | – | – | – |
| Feb-99 | | | | | | | | | | | – | – |
| Apr-99 | | | | | | | | | | | | – |
| Jun-99 | | | | | | | | | | | | |

Table A6.1. Pairwise comparisons on species diversity between different months of measurement (from January 1998 to June 1999) and treatment plots (chiselled vs hammered) of Nov-97 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Jan-98 | | Feb-98 | | Mar-98 | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Jan-98 | C | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | – | * | – | – |
| | H | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | – | * | – | – |
| Feb-98 | C | | | | – | – | – | – | – | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | * | – | * | * | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Mar-98 | C | | | | | | – | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Apr-98 | C | | | | | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| May-98 | C | | | | | | | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Jun-98 | C | | | | | | | | | | | | * | – | – | – | * | * | * | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | * | * | * | * | * | * | – | * | – | – | * | – | – | – | – | – |
| Aug-98 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | * | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | * | – | – | – |
| Jan-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

Table A6.2. Pairwise comparisons on species diversity between different months of measurement (from February 1998 to June 1999) and treatment plots (chiselled vs hammered) of Jan-98 clearings Student Neul ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Feb-98 | | Mar-98 | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Feb-98 | C | | – | * | * | * | * | – | – | * | * | * | * | * | * | * | * | * | * | – | – | * | – | * | * | – | – |
| | H | | | * | * | * | * | – | – | * | * | * | * | * | – | * | – | * | * | – | – | – | – | – | – | – | – |
| Mar-98 | C | | | | – | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| Apr-98 | C | | | | | | – | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| May-98 | C | | | | | | | | – | * | * | * | * | * | * | * | * | * | * | – | – | * | * | * | * | – | * |
| | H | | | | | | | | | * | * | * | * | * | * | * | * | * | * | – | – | – | – | – | – | – | – |
| Jun-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | * | * | – | – | – | – | * | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | * | * | – | – | – | – | * | – |
| Aug-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | * | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | * | * | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | | | | | – | – | – | – | – | – | * | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | | | | | | | | | – | * | * | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | * | * | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | | | | | |

Table A6.3. Pairwise comparisons on species diversity between different months of measurement (from March 1998 to June 1999) and treatment plots (chiselled vs hammered) of Feb-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Mar-98 | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Mar-98 | C | | – | * | * | – | * | * | * | * | * | – | – | * | * | * | * | * | * | – | * | – | – |
| | H | | | * | * | – | – | * | * | * | * | – | – | – | * | * | * | * | * | – | * | – | – |
| Apr-98 | C | | | | – | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| | H | | | | | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| May-98 | C | | | | | | – | * | * | * | * | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Jun-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | * | * |
| Aug-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | * | * |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | * | * |
| Nov-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | |

Table A6.4. Pairwise comparisons on species diversity between different months of measurement (from April 1998 to June 1999) and treatment plots (chiselled vs hammered) of Mar-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Apr-98 | | May-98 | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Apr-98 | C | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | – | – | * | * | * | * | – | – | * | * | – | – | – | * | * | – | – | – | * | * |
| May-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Jun-98 | C | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Aug-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | | | | | |

Table A6.5. Pairwise comparisons on species diversity between different months of measurement (from June 1998 to June 1999) and treatment plots (chiselled vs hammered) of May-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Jun-98 | | Aug-98 | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Jun-98 | C | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – | – | – | * | – | – | – | * | – | – | – |
| Aug-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Nov-98 | C | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | | | | | – | – | – | – | * | – |
| Mar-99 | C | | | | | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | | | | | |

Table A6.6. Pairwise comparisons on species diversity between different months of measurement (from November 1998 to June 1999) and treatment plots (chiselled vs hammered) of Aug-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Nov-98 | | Dec-98 | | Jan-99 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H | C | H | C | H |
| Nov-98 | C | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – | – | – | – | – | – | – |
| Dec-98 | C | | | | – | – | – | – | – | – | – | – | – | – | – |
| | H | | | | | – | – | – | – | – | – | – | – | – | – |
| Jan-99 | C | | | | | | – | – | – | – | – | – | – | – | – |
| | H | | | | | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | | | | | – | – | – | – | – | – | – |
| | H | | | | | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | | | | | – | – | – | – | – |
| | H | | | | | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | | | | | – | – | – |
| | H | | | | | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | | | | | – |
| | H | | | | | | | | | | | | | | |

Table A6.7. Pairwise comparisons on species diversity between different months of measurement (from December 1998 to June 1999) and treatment plots (chiselled vs hammered) of Nov-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Dec-98 | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H | C | H |
| Dec-98 | C | | – | * | – | – | – | – | – | – | – |
| | H | | | – | – | – | – | – | – | – | – |
| Feb-99 | C | | | | – | – | – | – | – | * | – |
| | H | | | | | – | – | – | – | – | – |
| Mar-99 | C | | | | | | – | – | – | – | – |
| | H | | | | | | | – | – | – | – |
| Apr-99 | C | | | | | | | | – | – | – |
| | H | | | | | | | | | – | – |
| Jun-99 | C | | | | | | | | | | – |
| | H | | | | | | | | | | |

Table A6.8. Pairwise comparisons on species diversity between different months of measurement (from February to June 1999) and treatment plots (chiselled vs hammered) of Dec-98 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H |
| Feb-99 | C | | – | – | – | – | – | * | * |
| | H | | | – | – | – | – | – | – |
| Mar-99 | C | | | | – | – | – | * | * |
| | H | | | | | – | – | – | – |
| Apr-99 | C | | | | | | – | * | – |
| | H | | | | | | | – | – |
| Jun-99 | C | | | | | | | | – |
| | H | | | | | | | | |

Table A6.9. Pairwise comparisons on species diversity between different months of measurement (from February to June 1999) and treatment plots (chiselled vs hammered) of Jan-99 clearings by Student-Newman-Keuls Method ('C' – chiselled plots; 'H' – hammered plots). Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Feb-99 | | Mar-99 | | Apr-99 | | Jun-99 | |
|---|---|---|---|---|---|---|---|---|---|
| | | C | H | C | H | C | H | C | H |
| Feb-99 | C | | – | – | – | – | – | – | – |
| | H | | | – | * | – | – | – | – |
| Mar-99 | C | | | | – | – | – | – | – |
| | H | | | | | * | * | * | * |
| Apr-99 | C | | | | | | – | – | – |
| | H | | | | | | | – | – |
| Jun-99 | C | | | | | | | | – |
| | H | | | | | | | | |

Table A7.1. Pairwise comparisons on species diversity between different clearing plots (Nov-97 and Jan-98) and control plots in the same month of measurement (February 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Control |
|---|---|---|---|
| Nov-97 | | * | – |
| Jan-98 | | | * |
| Control | | | |

Table A7.2. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98 and Feb-98) and control plots in the same month of measurement (March 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Control |
|---|---|---|---|---|
| Nov-97 | | – | * | – |
| Jan-98 | | | * | – |
| Feb-98 | | | | – |
| Control | | | | |

Table A7.3. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98 and Mar-98) and control plots in the same month of measurement (April 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Control |
|---|---|---|---|---|---|
| Nov-97 | | – | – | * | – |
| Jan-98 | | | – | – | – |
| Feb-98 | | | | – | – |
| Mar-98 | | | | | – |
| Control | | | | | |

Table A7.4. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98 and Apr-98) and control plots in the same month of measurement (May 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | Control |
|---|---|---|---|---|---|---|
| Nov-97 | | – | * | * | * | – |
| Jan-98 | | | – | – | * | – |
| Feb-98 | | | | – | – | – |
| Mar-98 | | | | | – | – |
| Apr-98 | | | | | | – |
| Control | | | | | | |

Table A7.5. Pairwise comparisons on species divesity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98 and May-98) and control plots in the same month of measurement (June 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Control |
|---|---|---|---|---|---|---|---|
| Nov-97 | | * | * | * | * | – | – |
| Jan-98 | | | – | – | – | – | * |
| Feb-98 | | | | – | – | – | * |
| Mar-98 | | | | | – | – | * |
| Apr-98 | | | | | | – | * |
| May-98 | | | | | | | – |
| Control | | | | | | | |

Table A7.6. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98 and Aug-98) and control plots in the same month of measurement (November 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Control |
|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | * | – | – |
| Jan-98 | | | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | * | – |
| Mar-98 | | | | | – | – | – | – |
| Apr-98 | | | | | | – | – | – |
| May-98 | | | | | | | * | – |
| Aug-98 | | | | | | | | – |
| Control | | | | | | | | |

Table A7.7. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98 and Nov-98) and control plots in the same month of measurement (December 1998) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Control |
|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | – | – | – |
| Mar-98 | | | | | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – |
| May-98 | | | | | | | – | – | – |
| Aug-98 | | | | | | | | – | – |
| Nov-98 | | | | | | | | | – |
| Control | | | | | | | | | |

Table A7.8. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Mar-98, Apr-98 and May-98) and control plots in the same month of measurement (January 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Mar-98 | Apr-98 | May-98 | Control |
|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – |
| Jan-98 | | | * | – | – | * |
| Mar-98 | | | | – | – | – |
| Apr-98 | | | | | – | – |
| May-98 | | | | | | – |
| Control | | | | | | |

Table A7.9. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98, Nov-98, Dec-98 and Jan-99) and control plots in the same month of measurement (February 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | – | – | – | – | – |
| Mar-98 | | | | | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – |
| Dec-98 | | | | | | | | | | – | – |
| Jan-99 | | | | | | | | | | | – |
| Control | | | | | | | | | | | |

Table A7.10. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98, Nov-98, Dec-98, Jan-99, Feb-99 and Mar-99) and control plots in the same month of measurement (April 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Mar-99 | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | – | – | – | – | – | – | – |
| Feb-98 | | | | – | – | – | – | – | – | – | – | – | – |
| Mar-98 | | | | | – | – | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | * | – | – |
| Aug-98 | | | | | | | | – | – | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – | – | – |
| Dec-98 | | | | | | | | | | – | * | – | – |
| Jan-99 | | | | | | | | | | | – | – | – |
| Feb-99 | | | | | | | | | | | | – | * |
| Mar-99 | | | | | | | | | | | | | – |
| Control | | | | | | | | | | | | | |

Table A7.11. Pairwise comparisons on species diversity between different clearing plots (Nov-97, Jan-98, Feb-98, Mar-98, Apr-98, May-98, Aug-98, Nov-98, Dec-98, Jan-99, Feb-99, Mar-99 and Apr-99) and control plots in the same month of measurement (June 1999) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Mar-99 | Apr-99 | Control |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | * | * | * | * | * | * | * | * | * | * | * |
| Jan-98 | | | – | * | * | * | * | * | * | * | * | * | * | * |
| Feb-98 | | | | * | * | * | * | * | * | * | * | * | * | * |
| Mar-98 | | | | | – | – | – | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – | – | – | – |
| Dec-98 | | | | | | | | | | – | – | – | – | – |
| Jan-99 | | | | | | | | | | | – | – | – | – |
| Feb-99 | | | | | | | | | | | | – | – | – |
| Mar-99 | | | | | | | | | | | | | – | – |
| Apr-99 | | | | | | | | | | | | | | – |
| Control | | | | | | | | | | | | | | |

Table A8. Pairwise comparisons on the first record of species diversity between different clearing plots (pooled data) by Dunn's Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Nov-97 | Jan-98 | Feb-98 | Mar-98 | Apr-98 | May-98 | Aug-98 | Nov-98 | Dec-98 | Jan-99 | Feb-99 | Mar-99 | Apr-99 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov-97 | | – | – | – | – | – | – | – | – | – | – | – | – |
| Jan-98 | | | – | – | – | – | * | * | – | – | * | – | * |
| Feb-98 | | | | – | * | – | * | * | – | – | * | – | * |
| Mar-98 | | | | | – | – | – | – | – | – | – | – | – |
| Apr-98 | | | | | | – | – | – | – | – | – | – | – |
| May-98 | | | | | | | – | – | – | – | – | – | – |
| Aug-98 | | | | | | | | – | – | – | – | – | – |
| Nov-98 | | | | | | | | | – | – | – | – | – |
| Dec-98 | | | | | | | | | | – | – | – | – |
| Jan-99 | | | | | | | | | | | – | – | – |
| Feb-99 | | | | | | | | | | | | – | – |
| Mar-99 | | | | | | | | | | | | | – |
| Apr-99 | | | | | | | | | | | | | |

Table B1. Pairwise comparisons on species richness among biweekly-retrieved tiles in A Ma Wan at different dates of retrieval using Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | | | | | | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 26-Feb | 12-Mar | 26-Mar | 9-Apr | 29-Apr | 19-May | 15-Jun | 15-Jul | 20-Aug | 22-Sep | 26-Oct | 26-Nov | 17-Dec | 14-Jan | 9-Feb | 4-Mar | 25-Mar | 22-Apr | 11-May | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 26-Feb | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 26-Mar | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 29-Apr | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 19-May | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 15-Jun | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 15-Jul | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| | 20-Aug | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | 22-Sep | | | | | | | | | | | | – | – | * | * | – | – | – | – | – | * |
| | 26-Oct | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | 26-Nov | | | | | | | | | | | | | | * | – | – | – | – | – | – | – |
| | 17-Dec | | | | | | | | | | | | | | | – | – | – | – | – | * | – |
| 1999 | 14-Jan | | | | | | | | | | | | | | | | – | – | – | – | * | – |
| | 9-Feb | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | 4-Mar | | | | | | | | | | | | | | | | | | – | – | – | – |
| | 25-Mar | | | | | | | | | | | | | | | | | | | – | – | – |
| | 22-Apr | | | | | | | | | | | | | | | | | | | | – | – |
| | 11-May | | | | | | | | | | | | | | | | | | | | | * |
| | 29-May | | | | | | | | | | | | | | | | | | | | | |

Table B2. Pairwise comparisons on species richness among monthly-retrieved tiles in A Ma Wan at different dates of retrieval using Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 12-Mar | 9-Apr | 19-May | 15-Jul | 22-Sep | 26-Nov | 14-Jan | 4-Mar | 22-Apr | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | – | – | – | * | – | – | – | – |
| | 19-May | | | | | – | – | – | – | – | – | – |
| | 15-Jul | | | | | | – | – | – | – | – | – |
| | 22-Sep | | | | | | | – | – | – | – | – |
| | 26-Nov | | | | | | | | – | – | – | * |
| 1999 | 14-Jan | | | | | | | | | – | – | – |
| | 4-Mar | | | | | | | | | | – | – |
| | 22-Apr | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | |

Table B3. Pairwise comparisons on mean density among biweekly-retrieved tiles in A Ma Wan at different dates of retrieval using Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | | | | | | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 26-Feb | 12-Mar | 26-Mar | 9-Apr | 29-Apr | 19-May | 15-Jun | 15-Jul | 20-Aug | 22-Sep | 26-Oct | 26-Nov | 17-Dec | 14-Jan | 9-Feb | 4-Mar | 25-Mar | 22-Apr | 11-May | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 26-Feb | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 26-Mar | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 29-Apr | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 19-May | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | * |
| | 15-Jun | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | * |
| | 15-Jul | | | | | | | | | | – | – | – | – | – | – | – | – | * | – | – | * |
| | 20-Aug | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | 22-Sep | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| | 26-Oct | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | 26-Nov | | | | | | | | | | | | | | – | – | – | – | – | – | – | * |
| | 17-Dec | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| 1999 | 14-Jan | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| | 9-Feb | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | 4-Mar | | | | | | | | | | | | | | | | | | – | – | – | – |
| | 25-Mar | | | | | | | | | | | | | | | | | | | – | – | – |
| | 22-Apr | | | | | | | | | | | | | | | | | | | | – | – |
| | 11-May | | | | | | | | | | | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | | | | | | | | | | | |

Table B4. Pairwise comparisons on mean density among monthly-retrieved tiles in A Ma Wan at different dates of retrieval using Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 12-Mar | 9-Apr | 19-May | 15-Jul | 22-Sep | 26-Nov | 14-Jan | 4-Mar | 22-Apr | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | – | – | – | – | – | – | – | – |
| | 19-May | | | | | – | – | – | – | * | * | * |
| | 15-Jul | | | | | | – | – | – | – | – | – |
| | 22-Sep | | | | | | | – | – | – | – | – |
| | 26-Nov | | | | | | | | – | – | – | * |
| 1999 | 14-Jan | | | | | | | | | – | – | – |
| | 4-Mar | | | | | | | | | | – | – |
| | 22-Apr | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | |

Table B5. Pairwise comparisons on percentage cover of encrusting coralline algae among biweekly-retrieved tiles in A Ma Wan at different dates of retrieval using Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | | | | | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 26-Feb | 12-Mar | 26-Mar | 9-Apr | 29-Apr | 19-May | 15-Jun | 15-Jul | 20-Aug | 22-Sep | 26-Oct | 26-Nov | 17-Dec | 14-Jan | 9-Feb | 4-Mar | 25-Mar | 22-Apr | 11-May | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | – | – | – | – | * | * | – | – | – | – | – | – | – | – | – |
| | 26-Feb | | | – | – | – | – | – | – | – | – | * | * | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 26-Mar | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | | | – | – | – | – | – | * | * | – | – | – | – | – | – | – | – | – |
| | 29-Apr | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 19-May | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 15-Jun | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 15-Jul | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| | 20-Aug | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | 22-Sep | | | | | | | | | | | | – | – | * | – | – | – | * | – | – | – |
| | 26-Oct | | | | | | | | | | | | | – | * | – | – | – | * | – | – | – |
| | 26-Nov | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| | 17-Dec | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| 1999 | 14-Jan | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| | 9-Feb | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | 4-Mar | | | | | | | | | | | | | | | | | | – | – | – | – |
| | 25-Mar | | | | | | | | | | | | | | | | | | | – | – | – |
| | 22-Apr | | | | | | | | | | | | | | | | | | | | – | – |
| | 11-May | | | | | | | | | | | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | | | | | | | | | | | |

Table B6. Pairwise comparisons on percentage cover of encrusting coralline algae among monthly-retrieved tiles in A Ma Wan at different dates of retrieval using Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 12-Mar | 9-Apr | 19-May | 15-Jul | 22-Sep | 26-Nov | 14-Jan | 4-Mar | 22-Apr | 29-May |
| 1998 | 15-Feb | | – | – | – | – | * | * | – | – | – | – |
| | 12-Mar | | | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | – | – | * | * | – | – | – | – |
| | 19-May | | | | | – | – | – | – | – | – | – |
| | 15-Jul | | | | | | – | – | – | – | – | – |
| | 22-Sep | | | | | | | – | – | – | – | – |
| | 26-Nov | | | | | | | | – | – | – | – |
| 1999 | 14-Jan | | | | | | | | | – | – | – |
| | 4-Mar | | | | | | | | | | – | – |
| | 22-Apr | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | |

Table B7. Pairwise comparisons on species diversity among biweekly-retrieved tiles in A Ma Wan at different dates of retrieval in by Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | | | | | | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 26-Feb | 12-Mar | 26-Mar | 9-Apr | 29-Apr | 19-May | 15-Jun | 15-Jul | 20-Aug | 22-Sep | 26-Oct | 26-Nov | 17-Dec | 14-Jan | 9-Feb | 4-Mar | 25-Mar | 22-Apr | 11-May | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | * | * | * | – | – | – | – | – | – | – | – | – | – | – | * |
| | 26-Feb | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 26-Mar | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | | | – | * | * | * | – | – | – | – | – | – | – | – | – | – | – | * |
| | 29-Apr | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 19-May | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 15-Jun | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – | – |
| | 15-Jul | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – | – |
| | 20-Aug | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – | – |
| | 22-Sep | | | | | | | | | | | | – | – | – | – | – | – | – | – | – | – |
| | 26-Oct | | | | | | | | | | | | | – | – | – | – | – | – | – | – | – |
| | 26-Nov | | | | | | | | | | | | | | – | – | – | – | – | – | – | – |
| | 17-Dec | | | | | | | | | | | | | | | – | – | – | – | – | – | – |
| 1999 | 14-Jan | | | | | | | | | | | | | | | | – | – | – | – | – | – |
| | 9-Feb | | | | | | | | | | | | | | | | | – | – | – | – | – |
| | 4-Mar | | | | | | | | | | | | | | | | | | – | – | – | – |
| | 25-Mar | | | | | | | | | | | | | | | | | | | – | – | – |
| | 22-Apr | | | | | | | | | | | | | | | | | | | | – | – |
| | 11-May | | | | | | | | | | | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | | | | | | | | | | | |

Table B8. Pairwise comparisons on species diversity among monthly-retrieved tiles in A Ma Wan at different dates of retrieval in by Dunn's Method for Kruskal Wallis One Way ANOVA on Ranks. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | 1998 | | | | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 15-Feb | 12-Mar | 9-Apr | 19-May | 15-Jul | 22-Sep | 26-Nov | 14-Jan | 4-Mar | 22-Apr | 29-May |
| 1998 | 15-Feb | | – | – | – | – | – | – | – | – | – | – |
| | 12-Mar | | | – | – | – | – | – | – | – | – | – |
| | 9-Apr | | | | * | – | – | – | – | – | – | * |
| | 19-May | | | | | – | – | – | – | – | – | – |
| | 15-Jul | | | | | | – | – | – | – | – | – |
| | 22-Sep | | | | | | | – | – | – | – | – |
| | 26-Nov | | | | | | | | – | – | – | – |
| 1999 | 14-Jan | | | | | | | | | – | – | – |
| | 4-Mar | | | | | | | | | | – | – |
| | 22-Apr | | | | | | | | | | | – |
| | 29-May | | | | | | | | | | | |

Table C1.1. Pairwise comparisons on mean percentage frequency between different survey sites (shallow water, deep water and –10 m CD) and seasons (fall, winter, spring and summer) in A Ma Wan by Student-Newman-Keuls Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | | Shallow water | | | | Deep water | | | | –10 m CD | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer |
| Shallow water | Fall | | – | * | – | – | – | – | – | – | – | – | – |
| | Winter | | | * | – | – | – | – | – | – | – | – | – |
| | Spring | | | | * | * | * | – | * | * | * | * | * |
| | Summer | | | | | – | – | – | – | – | – | – | – |
| Deep water | Fall | | | | | | – | – | – | – | – | – | – |
| | Winter | | | | | | | – | – | – | – | – | – |
| | Spring | | | | | | | | – | – | – | – | – |
| | Summer | | | | | | | | | – | – | – | – |
| –10 m CD | Fall | | | | | | | | | | – | – | – |
| | Winter | | | | | | | | | | | – | – |
| | Spring | | | | | | | | | | | | – |
| | Summer | | | | | | | | | | | | |

Table C1.2. Pairwise comparisons on species diversity between different seasons (fall, winter, spring and summer) in A Ma Wan by Student-Newman-Keuls Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Fall | Winter | Spring | Summer |
|---|---|---|---|---|
| Fall | | – | * | * |
| Winter | | | * | * |
| Spring | | | | – |
| Summer | | | | |

Table C2.1. Pairwise comparisons on mean percentage frequency between different seasons (fall, winter, spring and summer) in Lung Lok Shui by Student-Newman-Keuls Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Fall | Winter | Spring | Summer |
|---|---|---|---|---|
| Fall | | * | * | * |
| Winter | | | * | * |
| Spring | | | | * |
| Summer | | | | |

Table C2.2. Pairwise comparisons on species diversity between different seasons (fall, winter, spring and summer) in Lung Lok Shui by Student-Newman-Keuls Method. Significant difference ($p < 0.05$) is indicated by an asterisk (*).

| | Fall | Winter | Spring | Summer |
|---|---|---|---|---|
| Fall | | – | * | – |
| Winter | | | * | – |
| Spring | | | | – |
| Summer | | | | |

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